ON THE MORPHOLOGY OF THE EXCRETORY ORGANS OF METAZOA: A CRITICAL REVIEW.

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The desire to acquaint myself with modern ideas as to the homologies of the excretory organs has led to the present review. These organs constitute a chapter in comparative anatomy that is one of the most compendious and intricate of all. Their relations are so broad and manifold that no morphologist can go far without touching upon them, and one need not wonder at this because their function is above all others necessary to the continuance of the life of the individual.

Among those who have contributed largely to this subject are Balfour, Bergh, Bürger, Cuénot, Eisig, Goodrich, Hatschek, Lang, Eduard Meyer, Sedgwick and Vejdovský, but the bibliography shows how many well-known investigators have added to our knowledge. There is a wealth of accumulated facts that have never been treated critically in their entirety, and on that account the present bringing together of them may be of help to future students.

This memoir is divided into two portions: (*A*) a descriptive one, in which the groups of Metazoa and their particular excretory organs are treated in succession; and (*B*) a comparative one, in which all the excretory organs are reduced to certain types, and then the homologies of these discussed. It is in this second part that a standpoint is reached different, so far as I know, from previous ones, one that I hope puts the facts in a clearer light.

A. DESCRIPTIVE.

The following is a brief summary of our knowledge of the general structure and embryogeny of special excretory organs considered separately for each group. Histological details are not entered upon. I have endeavored to consult all the more important literature up to 1907, but at the same time to refer in the citations to only the more comprehensive accounts; the literature references therefore do not by any means represent complete bibliographies, but refer the reader to the more important memoirs.

The Orthonectida, Dicyemida, Cnidaria and Porifera lack special excretory organs; and such structures are still unknown for *Cephalodiscus, Rhabdopleura,* the Chaetosomatidæ, Desmoscolicidæ, and Pentastomida.

1. CTENOPHORA.

Here there are short, presumably entoblastic, canals that connect the aboral canal (funnel canal) of the gastro-vascular cavity with the aboral surface of the body; there may be two or four of these openings; these discharge injected carmine, while there is no evidence that water is taken in through them (Chun, 1880).

2. PLATHELMINTHES.

These possess branching, tubular organs whose finest branches (capillaries) have intracellular cavities and terminate in closed flame cells, the latter being very small and numerous. Nothing is known as to their embryonic origin, except the one observation of Lang (1884) that in Polyclades a pair of solid ingrowths of the ectoblast seems to represent their beginnings. The main structural variations are with regard to the number, ramification and degree of anastomosis of the main canals, and the number and position of nephridiopores and excretory canals.

(1) *Turbellaria.*

Polycladidea.—Discovered by Max Schultze (1854) these organs have received subsequent description only by Lang (1884), who found that the terminal flames are unicellular and who could trace the supposed excretory canals of *Thysanozoon* to the dorsum, but could not find their openings there. Accordingly, a complete knowledge of their structure is still a desideratum. I have not been able to find them on sectioned material.

Rhabdocœlida.—Here they appear to be absent only in the

Acœla. Three chief types have been distinguished (v. Graff, 1882): a single main canal with a single nephridiopore (*Stenostoma*); a pair of main canals with independent nephridiopores, and a pair of main canals with a common nephridiopore. In *Bothrioplana* (Vejdovský, 1895) there are two pores different in structure, one at the middle and the other at the anterior end of the body; into the former open two main canals, each of the latter divides into an anterior and a posterior branch, and these anterior branches connect also with the anterior nephridiopore. In the Eumesostomina (Luther, 1904) the main canals open independently either on the surface of the body, or into the mouth, or into the genital atrium (all these being ectoblastic), and besides the terminal flame cells there are other flames (without nuclei) interpolated in the course of the canals. In these forms there is never more than one pair of main canals, or more than two nephridopores.

Tricladidea.—In *Planaria* but more specially *Gunda* Lang (1881) described two main ducts on each side of the body, each bearing numerous capillaries ending in flame cells; there are anastomoses between the former but not between the latter; from each main duct proceeds a series of excretory ducts each of which opens dorsally by a small contractile vesicle. And Böhmig (1906) adds to this account of *Gunda* by the discovery of four pairs of main canals, and of ventral as well as dorsal nephridiopores. In *Dendrocœlum* Ijima (1885) found similar relations, though he held there to be but one main canal on each side; while Wilhelmi (1906) found two of them with a segmental arrangement of eight pairs of excretory ducts, and (in opposition to the earlier observations of Chichkoff) no openings into the pharynx. The Tricladidea differ from the Rhabdocœlida in the presence of numerous serial excretory ducts.

(2) *Trematoda.*

The chief characteristic of the excretory organs is their dendritic branching and their degree of anastomosis. In the Monogenea there are usually paired nephridiopores (in *Gyrodactylus* a single one) placed in most cases at the anterior end but sometimes at the posterior. The excretory vesicle of the Digenea is at the posterior end, terminal or dorsal, and into it open usually two but sometimes four or even six main canals (Braun, 1893). In the larva (miracidium) of *Distomum* there is a single large flame cell on each side of the body with a capillary opening on the surface (Coe, 1896). Bugge (1902) has shown that each flame cell and its capillary "develop out of one cell and are to be compared with a unicellular gland," a practical confirmation of Lang's (1884) suggestion.

(3) *Temnocephaleæ.*

The excretory system of these curious forms has been made known particularly by Weber (1889). There is a pair of separated dorsal nephridiopores, each communicating with main canals that branch and anastomose with those of the opposite side, so that the general arrangement is like that of the Trematoda.

(4) *Cestoda.*

Here the main canals have no dendritic branching but frequent anastomoses, so that quite generally each proglottid has one or two pairs of transverse canals connecting the main lateral ones; the main lateral canals open by a common contractile vesicle at the posterior end of the ripest proglottid (Pintner, 1896). In the most detailed contribution on the subject (Bugge, 1902) muscle fibrils of the main canals are described and also valves within them (the latter discovered by Köhler in 1894); in the cysticercus stage foramina secondaria were found connecting the main canals with the surface of the body. Bugge uses the term "Wimperflamme" to include the "Terminalzelle" ("Geisselzelle, Deckzelle"), with the "Wimper" and "Trichter" and "Capillare." He traced such Wimperflammen as outgrowths from the walls of the main canals: a cell of the latter projects outwards then divides into a group of four; of these four one forms three Trichter and the capillary (the cavities of these parts being intracellular), while each of the three others becomes a flame cell with a ciliary flame.

Anatomically considered there are two main kinds of excretory organs in the Platyhelminthes: (1) with numerous serial excretory canals, found only in the Tricladidea; and (2) with only one or two excretory canals, found in all the others (though the relations are not yet known for the Polyclades).

3. NEMERTINI.

From the comprehensive treatment given by Bürger (1895), based largely upon his own researches, it follows that the excretory organs are as a rule in the form of two main canals parallel with the lateral blood vessels and not communicating together; each opens to the exterior of the body by one, or more rarely by a series of several (up to about forty), excretory ducts; the main canals are usually restricted to the region of the stomach, but in some genera they extend the length of the body. From them proceed delicate capillaries that terminate blindly in multicellular "Endkölbchen"; the latter may project into the walls of blood vessels, but (contrary to the earlier opinion of Oudemans) there is no open communication of any portion of the nephridia with these vessels or other internal cavities. In the freshwater *Stichostemma* I showed (1897) that an unusual condition obtains, in that in the adult instead of a single canal on each side there is a series of them, some with and some without excretory canals; and then Böhmig (1898) demonstrated that the latter are produced by a secondary segmentation of originally continuous ducts.[1] Punnett (1900) and Coe (1906) found in *Tæniosoma* besides excretory pores opening on the surface of the body others that connect with the œsophagus; the latter are clearly embryonic ducts persisting in the adult.

The larvæ do not possess special excretory organs. The definitive ones arise, according to Bürger, as a pair of hollow evaginations of the ectoblastic stomodæum of the larva, soon abstrict from the œsophagus and then open into the amniotic cavity at a ventral point near the mouth, a position quite different from that of the adult excretory pores. The origin of the latter is not known, and

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[1] I had described the terminal bulbs of this genus as closed from the capillaries, with an internal cuticular lining but no flame, while Böhmig found them essentially as described by Bürger except that each consists of usually not more than two cells. I have recently had opportunity to examine living material and to compare it with my former sections, and find I had overlooked the true flame cells and that Böhmig had described them correctly. Each terminal bulb consists of from one to five cells.

Bürger suggests they may either be secondary invaginations of the epidermis, " or the nephridium itself must break a new way through the body wall. Judging from the adult animal the first alternative must be the case."

4. GASTROTRICHA.

There is a single pair of much convoluted tubules, lateral from the intestine, opening near each other on the ventral surface without excretory vesicles. Each ends internally with a single closed bulb, but it is not determined whether it contains a single flagellum or a row of cilia (Zelinka, 1889).

5. ROTATORIA.

The excretory organs have been most carefully described for the Philodinidæ (Zelinka, 1886, 1888, 1891, Plate, 1889), Flosculariidæ (Montgomery, 1903, Gast, 1900), Melicertidæ (Hlava, 1904, 1905), Atrochidæ (Wierzejski, 1893) and Asplanchnidæ (Hudson and Gosse, 1886, Rousselet, 1891, Weber, 1898). There is always a right and left main canal; the flame cells may be directly attached to these (most Philodinidæ), but more usually are placed at the ends of capillaries, branches of a main capillary that open into the main canal at one or two points. The number of flame cells on eash side of the body is small, usually from three to six, and in that case they are relatively large; but in the Asplanchnidæ there are some fifty of them on each side sessile on a main capillary. Their great number here may be due to the large size of these species. The main canals unite posteriorly into a short unpaired duct that opens into the cloaca; and anteriorly they are usually connected by a transverse commissure (absent in some Philodinidæ). The main canals have an intracellular cavity, are composed of a few cells and are usually without cilia; terminal flame and capillary is a single cell, the termination of which is entirely closed from the body cavity and contains an internal flame of cilia and (in *Asplanchna*) has a couple of long flagella on the outer surface.

The early development of these structures has not been determined (Zelinka, 1891).

6. Endoprocta.

Joliet (1880) described for *Pedicellina* and *Loxosoma* a pair of short ciliated canals with a common nephridiopore, and with their inner ends open to the body cavity. Prouho (1890) leaves the question unsettled whether these ends are open or closed. All other observers describe the inner termination of each canal as closed by a flame cell: so Foettinger (1887) and Ehlers (1890) for *Pedicellina,* Harmer (1885, *Loxosoma*), and Davenport (1893, *Urnatella*). The cavity of these canals is intracellular, and only in *Loxosoma* are there paired nephridiopores.

Besides this "Chief excretory apparatus" Davenport found in the stalk of *Urnatella* "elongated spaces terminating blindly at one end in structures which must be regarded as flame cells . . . I have not, however, been able in any instance to trace an individual tubule to any considerable distance, or until it opens into any other organ."

Accordingly, all Endoprocta seem to have a pair of nephridia internally closed that do not serve as genital ducts, and in one genus flame cells seem to occur in the stalk.

In regard to their development, Hatschek (1877) found in the full-formed larva of *Pedicellina* a pair of ciliated canals like those of the adult, but did not determine either their structure or origin. It would seem probable that this excretory organ persists in the adult.

7. Rhodope.

For this curious form that has been variously related to the Turbellaria and the opisthobranch mollusks, Böhmig (1893) described a nephridiopore on the right side just anterior to the anus, into which opens a "Urinkammer"; into the latter discharge ramified ducts, and to each of these are attached about forty flame-bearing terminal organs, each completely closed from the body cavity and consisting of from four to eight cells. Nothing is known of the development.

8. Acanthocephala.

The excretory organs of this group are known only from the observations of Kaiser (1892, 1893). They occur only in the large *Echinorhynchus gigas* and seem to be absent in the smaller species (I also have looked for them in vain in a number of American species). In the female there is a pair of them discharging into the oviduct; each is a broad spade-shaped organ composed of three cells, the free end branched dendritically, each finest subdivision of which terminates in a perforated membrane bearing on the luminal side a tuft of long cilia; there are about five to six hundred of these terminal flames to each nephridium, though the whole organ it will be recollected is composed of only three cells. The Acanthocephala are specially characterized by the small number but great degree of specialization of their cells. In the male the nephridia open into the ductus ejaculatorius, and are similar to those of the female save that the terminal flames are less numerous. Kaiser supposes that in the smaller species lacking these organs the oviduct is excretory, since in them the uterus bell is open to the body cavity.

They arise conjointly with the genital ducts from the ectoblast.

9. CHÆTOGNATHA.

No excretory organs were found by Hertwig (1880), while Grassi (1883) suggests that a pair of small glands opening at the junction of the head and prepuce may be urinary.

The genital ducts are not comparable with nephridia because they do not develop until maturity, and because the vasa deferentia are ectoblastic and the oviducts are outgrowths of the ovaries (Doncaster, 1902).

10. KINORHYNCHA.

The genus *Echinoderes* exhibits one pair of short, pyriform canals, ciliated throughout, with enlarged closed inner ends, that open separately and dorso-laterally (Reinhard, 1887).

11. NEMATODA.

As first made known by Anton Schneider (1866) and confirmed by most subsequent writers there is usually an excretory duct in each lateral line (though one may be wanting) that extend from the posterior region of the body to the œsophagus, where they converge and open by a single median nephridiopore. The inner ends of these canals are closed, and each is lined by a cuticula. Four types of these have been distinguished according to their form and position of the nephridiopore (Jägerskiöld, 1898). A more careful description has been furnished by Goldschmidt (1906) for *Ascaris lumbricoides,* who found that the whole apparatus is composed of but two cells, with a single nucleus for both main canals and one for the anterior unpaired duct. Goldschmidt further considers these canals to be simply for discharge, and that a peculiar solid tissue of the lateral lines is the true secretory portion; these glandular masses are multinuclear and do not touch the walls of the canals, but fine pores appear to extend towards them from the lumina of the canals. In his own words: "The excretory system of *Ascaris* . . . consists of the excretory gland proper (analogous to a kidney) that lies within the lateral lines, and of the discharge duct (analogous to a ureter) that consists of two horseshoe-shaped limbs composed of a single cell and of an unpaired terminal portion represented by one cell."

Little is known of the development of these canals. They lie within the lateral lines, and Zur Strassen (1892) has shown that the latter are mesoblastic. Conte (1902) found the excretory apparatus to arise from a single mesoblast cell that becomes secondarily placed in the lateral line.

12. GORDIACEA.

For this group specific excretory organs are still unknown, though it has received much study. Vejdovský (1886, 1894) has interpreted the peri-intestinal cavity as excretory, but this has no opening to the exterior; and he has suggested that the oviducts and vasa deferentia are modified nephridia,—a conclusion drawn from his idea that the Gordiacea are degenerate annelids, a standpoint that has been combated by me (1903*a*). In late embryonic stages he found a "braune Drüse" opening into the intestine near the mouth; this is not found in the adult, unless the problematical supra-intestinal orgon described by me for *Paragordius* may be an excretory organ conveying fluids from the peri-intestinal space to the intestine. It is probable that excretion must take place through either the genital ducts or the intestine, since the thick cuticula on the surface of the body is hardly permeable.

The gland of the larva construed by Villot (1874) as an excretory organ has been considered by me (1904) to be rather a poison gland; I have shown that its body develops as an abstriction of the entoblast, and that its duct opens at the base of the proboscideal stilets; it is completely closed from the body cavity and does not possess cilia.[2]

13. ECTOPROCTA.

For the Phylactolæmata the fullest description is that of Cori (1893, *Cristatella*), according to whom there is a nephridium just above the anus, between the body wall and the peritoneum, consisting of two ciliated nephrostomes opening into the cœlom, connecting with an enlarged sac that has a single nephridiopore near the cerebral ganglion. He proved experimentally that lymphocytes ingest waste particles, and then are discharged by this organ.

In the Gymnolæmata there is in some species an organ discovered by Hincks (1880), and more fully described by Prouho (1892) who names it the "organe intertentaculaire"; this occurs only in sexual individuals, is primarily a genital duct, and is a ciliated canal with an inner nephrostome. In most Gymnolæmata special excretory organs are absent (Ostroumoff, 1886, Harmer, 1891). Harmer concludes from injection experiments that excretion is performed "partly by the cells which I have described as leucocytes, partly by the walls of the alimentary canal, and partly by the funicular tissue," while he and Ostroumoff have proved that the formation of the "brown body" and the death of the polypid is due to an accumulation of waste substances especially in the intestine.

The larvæ lack excretory organs, and the development of those of the adult has not been described.

14. SIPUNCULIDA.

There are as a rule two "excretory tubes," but within the same genus either two or one may occur. In most cases each of these has

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[2] In the marine *Nectonema*, that shows some similarity to the diplobiotic Gordiacea, excretory organs are unknown.

a nephridiopore on the ventral surface of the body, and a ciliated nephrostome placed at the inner end of the tube or else near the external opening. But in *Sternaspis* Goodrich (1897) found no nephridiopores, and in an immature individual of *Phascolosoma proki* Sluiter (1882*b*) found no nephrostomes. In all cases these serve as genital ducts. Metalnikoff (1900), in the most detailed memoir, concludes that the nephrostome cannot serve excretion but acts merely to swallow the germ cells, while excretion must be accomplished by osmosis through the wall of the organ that is lined by cells resembling the chloragogue of annelids. Goodrich holds these are not true nephridia, but "peritoneal funnels peculiarly modified."

The embryological data are conflicting. In *Phascolosoma* Gerould (1906) found no excretory organs in the trochophore, and in the "larva" (that succeeds the trochophore) the definitive nephridia arise as solid ectoblastic ingrowths ("a pair of ingrowths, probably of ectoderm"), to which are added funnels of mesoblastic origin. In *Sipunculus* Hatschek (1883) described a pair of "Nierenzellen" in the mesoblast of the embryo; each of these divides into four cells which acquire an intracellular cavity, then one end of each cell cord becomes attached to the ectoblast while the other opens into the cœlom. Gerould's account is the much more detailed and thorough, and renders it probable that both ectoblast and mesoblast enter into these nephridia. The trochophore lacks nephridia.

15. PRIAPULIDA.

For these animals we have only the brief description of Schauinsland (1886), unaccompanied by figures. From each side of the posterior end there is said to invaginate a pair of ectoblastic tubes. Then a series of short excretory tubules grow out from the walls of these; the "Endorgane" are multicellular, closed from the body cavity, each cell with a long flagellum. Still later other folds evaginate from the walls of the main ducts, and their cells become the reproductive elements. According to this description this would be a unique ectoblastic organ, not unlike that of the Plathelminthes, that proliferates germ cells.

16. PHORONIDEA.

In the adult just behind the transverse septum Cori (1890) found a pair of ciliated canals with open nephrostomes, and determined that their function is both genital and urinary. In *Phoronis australis* Benham (1889) found that each tube has two nephrostomes, and a similar relation was discovered by Cowles (1905).

There is quite general agreement that the larval nephridia are ectoblastic (Ikeda, 1901, Longchamps, 1902, Shearer, 1906, Cowles, 1905); from a nephridial pit at the posterior end grow out the two canals whose cavity is intercellular. The observers already cited together with Caldwell (1882) and Goodrich (1903), in contradiction to Masterman (1897), agree further that the nephridia of the actinotrocha are closed at their inner ends from the blastocoel in which they lie; and Shearer, who gives the most complete account of the development of these structures, shows that their inner ends are closed by a group of solenocytes that represent outgrowths from the tubes. Longchamps states that these larval organs persist into the adult; this is assumed by Shearer who decides that these canals "acquire openings into the cœlom by means of ciliated funnels of unknown origin"; while Ikeda concludes: "We may assume that the formation of the infraseptal nephridial funnels of the adult is due to secondary outgrowths of the infraseptal portion of the atrophied, larval nephridial canals." The only point not fully decided is that of the origin of the funnels.

17. BRACHIOPODA.

According to the monographs of Van Bemmelen (1883), Blochmann (1900) and Morse (1902) there is usually one pair of supposed excretory organs, with nephrostomes and nephridiopores, that serve as genital ducts; in *Hemithyris* and *Rhynchonella* there are two pairs.

Nothing is known of their development, and there appear to be no larval nephridia.

18. ECHINODERMATA.

Crinoidea.—Special excretory structures are unknown.

Echinoidea.—The axial organ (ovoid gland) has been considered an excretory organ (Hamann, 1887, Sarasin, 1888, Ludwig, 1889) and proved to be so by carmine injection (Kowalevsky, 1889), while to it has also been ascribed the function of producing cœlomic cells (Leipoldt, 1893). It is a slender axial sac, the oral end of which ends blindly, opening by a delicate canal under the madreporite close to the stone canal; it is composed of a meshwork of trabeculæ of connective tissue, covered internally by an epithelium, in the meshes of which lie amœboid cells (Ludwig). Hamann described its cavity as communicating with blood lacunæ and the Sarasins as connecting with the body cavity by nephrostomes, but these results have not been confirmed and the bulk of evidence points to its being closed from other body cavities.

Ophiuroidea.—Here both respiration and excretion take place osmotically through the walls of the genital bursæ (Cuénot, 1888).

Asteroidea.—By injection Kowalevsky (1889) found that the bodies of Tiedemann are the excretory organs of the ambulacral system. Cuénot (1901) distinguished (1) amœbocytes, floating cells in the cœlom, blood vessels and ambulacral system, that are first phagocytic, and when they become laden with excretory products leave the organism by passing through the walls of the gill sacs; and (2) nephrocytes. Of the latter he distinguished: those that take up indigo (epithelium of the intestinal cæca), and those that ingest carmine (peritoneum, epithelia of perihæmal spaces and ambulacral vessels, inner cells of septal organs).

Holothurioidea.—In the Synaptids the "ciliated funnels" have been proved to collect waste products, by their ciliary action and agglutinating secretion; such products and amœbocytes loaded with them become caught in these organs, and ultimately make their way through the solid tissues to become deposited beneath the skin (Schultz, 1895, Cuénot, 1902). These funnels are generally arranged in rows on either side of the mesenteric radix, and project into the cœlom either separately or in groups. Each is a somewhat spoon-shaped, flattened prominence, with a concave ciliated surface, attached to the wall of the cœlom by a slender stalk, both plate and stalk being composed of solid connective tissue covered by peritoneum. Thus they are really not funnels at all, but solid projections into the body cavity, and cannot in any way be compared with the peritoneal funnels (peritoneal evaginations) of other forms. In the Pedata the respiratory trees have been considered as in part excretory (Schultz, 1895); and the organs of Cuvier, tubes that also open into the cloaca behind the preceding, have been regarded as excretory by Hérouard (1893), but it is proven that these are rather eversible defensive structures (Minchin, 1892, Russo, 1889).

The ambulacral system of the echinoderms seems to mainly subserve locomotion, respiration and nutrition; but the bodies of Tiedemann, as mentioned above, that occur in it are excretory, and the Polian vesicle in holothurians may contain an "irregular non-living mass of brown spherules" which may be waste substances derived from the brown wandering cells occurring elsewhere in this system (Gerould, 1896).

The larvæ lack nephridia, and there appear to be no organs in this group comparable with excretory organs in others. The only representatives of peritoneal funnels are ciliated evaginations from the embryonic hydrocœl that join secondarily with ectoblastic invaginations; there is usually only one of these and it persists as the stone canal, but there may be two; Field (1892) compared the enterocœls with nephridia that have secondarily come into the service of locomotion.

There is little known of the development of the genital organs of Holothurioids. In Asteroids they have been described as coming from a solid mesenchyme mass that invaginates the peritoneum; only in Echinoids is the gonad stated to be peritoneal, a proliferation of cells of the left posterior enterocoel. Accordingly, there is no evidence that the gonads or their ducts stand in relation to nephridia.

15. TUNICATA.

Special organs of excretion fail in the Appendiculariæ (Seeliger, 1893), and I have not found them described for the Doliolidæ. For other forms Dahlgrün (1901) has distinguished the following kinds: (1) Scattered excretory cells, in the visceral region (in *Botryllus, Botrylloides, Polycyclus, Ciona, Salpa*); (2) vesicles, rather numerous in the connective tissue, each with a wall formed of prismatic cells and with fluid or solid contents (*Ascidiella,* *Ascidia*); (3) sacs, less numerous, on both sides of the body below the mantle, with walls of cubical cells (*Cynthia, Microcosmus*); and (4) renal organs, a single voluminous sac on the right side of the body with epithelial wall (*Molgula*). Todaro (1902*a, b*) described them for the Salpidæ as hollow vesicles in the number of three pairs, to which waste products are carried by the blood corpuscles.

Thus in the majority of Tunicates they are vesicles without ducts placed in the mesenchyme. Van Beneden and Julin (1886) found them to be derived from mesenchyme, and concluded that this embryonic tissue is a modification of what was ancestrally enterocœlic mesoblast; Conklin (1905), however, has shown that all the mesoblast is peristomial, consequently the tissue from which these organs develop may be mesectoblast.

The genital ducts are outgrowth of the gonads, therefore probably have no relation to nephridia.

16. DINOPHILEA.

Korschelt (1882) described for *Dinophilus apatris,* and Weldon (1887) for *D. gigas,* a nephridial system of the platyhelminthan type, though both of them saw clearly only the flame cells. Subsequent observations have demonstrated that there are metamerically arranged, separated nephridia. Thus Schimkewitsch (1895) found in *D. vorticoides* four pairs of these in the male and five pairs in the female; Harmer (1889) and Shearer (1906) for *D. tæniatus,* Nelson (1907) for *D. conklini,* and E. Meyer (1887) for *D. gyrociliatus* discovered five pairs. These are ciliated tubes each with its own nephridiopore, closed internally, and (according to Shearer) beset with solenocytes. In *D. conklini* the first pair is much more complex than the others and consists of a considerable number of cells; each of those of *D. gyrociliatus* is described by Meyer as consisting of only two cells.

Schimkewitsch considered the genital ducts of the male to be a fifth pair, and the corresponding ducts of the female to be a sixth pair of nephridia, and Harmer regarded the seminal vesicles as segmental organs. This is, however, little more than a supposition, since the genital ducts are quite different in structure from the nephridia and are in connection with the cœlom (genital chamber), and since the development of the nephridia is unknown.

The mid-gut has also been demonstrated to be excretory (Schimkewitsch, 1884).

17. Hirudinea.

Adult Meganephridia.—There is a series of separated pairs, less numerous than the somites. Nephrostomes may be lacking as in the case of five out of the seventeen pairs of *Hirudo* (McKim, 1895) the three most anterior pairs of *Nephelis* (Graf, 1893), and all of *Branchellion* (Bourne, 1884). Leuckart (1894) discovered the anatomical connection of the nephridia with the nephrostomes, and this has been corroborated by Voinov (1896), McKim, Graf and Schultze (1883), in opposition to the results of Bolsius (1892) that the "organes ciliés" have no connection with the loop. But even when they are connected there need not be an open communication between the two (Graf, 1899). When present the funnel lies in the segment preceding that of the loop. The cavity of the nephridia is much branched and intracellular. An excretory bladder may be present as a part of the excretory duct, but this is lacking in *Clepsine*.

The nephridia arise from segmentally arranged mesoblastic nephroblasts, that lie deep below the embryonic epidermis. Each of these divides into two cells, the anterior of which gives rise to the funnel and the posterior to a cord of cells that forms the secretory portion of the loop; the cavity into which the nephrostomes open is a true cœlom; the excretory ducts and vesicles are ectoblastic ingrowths (Bürger, 1891, 1894, 1902, Bergh, 1891, McKim, 1895). Bürger is very positive with regard to the mesoblastic origin of the nephridia, in opposition to the earlier view of Whitman (1887).

Adult Plectonephridia.—Bourne (1884) first found net-like nephridia in *Branchellion, Pontobdella* and *Piscicola;* in *Pontobdella* they consist of a network of canals extending from the ninth to the nineteenth segment, with ten pairs of nephridiopores, while in *Branchellion* they have only one pair of such openings. They have been redescribed by Johansson (1898), and I am acquainted with his account only from the citation given by Lang (1903, p. 103). "In *Pontobdella* the nephridia consist of very richly branched and reticularly anastomosing tubes, among which one cannot distinguish main trunks. The two nephridia of the same segment are many times joined together, and the nephridia of the several segments equally so. In *Cystobranchus* each nephridium has attained a complete independence and connects neither with the other nephridia of the same segment, nor with those of neighboring segments. It consists then also only of a single, coarse, unbranched tube. The remaining genera correspond in this relation more or less with *Pontobdella;* one can, however, always distinguish particular trunks. In *Piscicola* one part of the nephridium, that is much more strongly developed than the remaining part, corresponds exactly in position with the nephridium of *Cystobranchus*. *Pontobdella* departs, finally, from all the other genera in this, that the nephridia have inner openings." Nothing is yet known of the development of these reticular organs.

Genital Ducts.—These were considered by Nusbaum (1885) to be modified nephridia. Bürger first (1894) opposed this comparison, but later (1902) he maintained that the female genital apparatus and the terminal portions at least of the vasa deferentia are possibly homologous with nephridia in developing from gonoblasts that are homodynamous with nephroblasts.

Larval Nephridia.—In the Hirudinea three of the blastomeres of the 4-cell stage give rise to a larval body that later perishes, while the fourth blastomere alone produces the adult body (Brandes, 1901). This larval body produces no nephridia. The "Urnieren" arise from the germ band that develops within this larval body, and they last only as long as the latter does. Bergh (1884, 1901) has shown that there are three pairs of these in *Aulastoma* and *Hirudo* and two pairs in *Nephelis,* all developing from the germ band; and he and Sukatchoff (1900) demonstrated that the inner ends are closed and the cavity intracellular. These larval nephridia arise from cell rows of the germ band that are generally considered mesoblastic, though this point is hardly finally settled.

Excretophores.—Excretory cells within the connective tissue

(Graf, 1899), that develop from the splanchnic layer of the mesoblast (Bürger, 1902).

Chloragogue (*Botryoïdal Tissue*).—Excretory cells placed upon the blood vessels (Graf, 1893).

18. OLIGOCHÆTA.

Adult Nephridia.—There are two main kinds of these which it will be convenient to consider separately: *meganephridia,* larger and in separated pairs; and *plectonephridia,* networks of smaller nephridia.

Meganephridia.—Of these there is usually one pair to each trunk segment, though exceptions are very numerous; each has a preseptal open funnel and a postseptal loop with intracellular cavity; their nephridiopores are usually separated and placed latero-ventral. The smallest number known is two pairs (*Bdellodrilus,* Moore, 1897). In *Brachydrilus* there are two pairs to each somite (Benham, 1888). The anterior five pairs open into the pharynx in *Dichogaster* (Beddard, 1888*b*), and probably also in *Eminea* (according to Benham, 1890*b*, who terms this a "peptonephridium"). In *Limnodrilus* the two anterior pairs perforate septa while the others do not (Rybka, 1899). *Libyodrilus* is characterized by the nephridia opening into a tubular system situated in the musculature, consisting of four main longitudinal vessels extending from segment to segment and of segmental ring vessels, there being numerous excretory ducts from the latter; this integumental network is secondary and develops after hatching (Beddard, 1891). Numerous other deviations from the general type are known that it is not necessary to mention here, beyond the fact that nephrostomes are lacking in the Chætogastrids (Vejdovský, 1885).

Plectonephridia.—A plectonephridium is a complex that in each segment is composed of numerous micronephridia, without nephrostomes, that are joined by a network of canals. In *Acanthodrilus* there is one such micronephridium to each of the eight setæ of each posterior segment, and in each anterior segment there are about one hundred nephridiopores; somewhat similar relations obtain in *Typhæus* (Beddard, 1888*a*). In *Megascolides* there are a great number of bundles of micronephridia which clothe the body wall except medially, these opening into a network of intracellular ducts placed outside of the peritoneum, and the latter discharge at the surface by irregularly arranged canals (Spencer, 1889). In *Mahbenus* each micronephridium has its own excretory duct (Bourne, 1894). The network of fine canals may be continuous from segment to segment, as in *Perichæta,* or only the micronephridia of one and the same segment may be so connected as exemplified by *Deinodrilus, Acanthodrilus,* and *Dichogaster* (Beddard, 1888*b*).

Both of these kinds of nephridia may occur in the same animal and even in the same segment, as in *Megascolides;* and in this genus there is a pair of ventral longitudinal canals continuous from segment to segment into which both open (Spencer). In *Dichogaster* the posterior segments contain both kinds (Beddard, 1888*b*).

Development of the Meganephridia.—With great hesitation I attempt to give a brief review of this subject, that has proved the Austerlitz of many a theory. Kowalevsky (1871) was the first to demonstrate the mesoblastic origin of these organs in *Euaxes* (*Rhynchelmis*) and *Lumbricus.* Vejdovský and Bergh have furnished more observations on the subject than any other writers. Vejdovský's results (1885, 1892*a,* 1900) on *Rhynchelmis, Stylaria* and *Tubifex* are as follows: Each nephridium arises from three separated anlages: (1) A large preseptal funnel cell, giving rise to the nephrostome; (2) a cord of small cells budded off behind the former, producing the secretory loop; and (3) an ectoblastic invagination that joins with the latter and forms the distal canal and the excretory vesicle. Bergh's studies (1888, 1890, 1899) on *Lumbricus, Criodrilus* and *Rhynchelmis* differ from those of Vejdovský mainly in deriving each nephridium from a single mesoblastic anlage instead of from three parts; in his mind the organ is essentially an embryonic unit. Wilson (1889) concluded for *Allolobophora* that the funnel arises from a large mesoblast cell, and the loop from a postseptal mass of cells that is continuous with the ectoblastic nephridial cell cords, though he admits the loop may nevertheless be mesoblastic. And Lehman (1887, *Allolobophora*) derived the nephridium from a large preseptal cell.

These researches agree in finding that the nephridia arise segmentally, to which the conclusions of Roule (1889) alone are opposed, and that their first beginning is the preseptal funnel cell. But there is considerable conflict of opinion as to what germ layer produces these cells and the cords that arise behind them. They arise in that cell row of the germ band formed by proliferation of the posterior nephroblasts. The germ band is covered by a thin ectoblast, and the funnel cells lie at points where the mesoblastic dissepiments meet the ectoblast; they are blastocœlic in position. Bergh is positive that funnel cells and nephridial cords are mesoblastic, derived from what he terms the "innere Muskelplatten," and Lehmann and Roule express the same opinion. Wilson hesitates to decide whether the nephridial cords are ectoblastic, though he ascribes this origin to the funnel cells. Vejdovský considers that at this early stage of the embryo, when these parts are first definable, there is no mesoblast but only the two primary germ layers and that the funnel cells may have emigrated from the ectoblast. It is to be noted in this connection that the funnel cells when they are first distinguishable have never been seen actually in the ectoblast, but always beneath it. And the nephridial development is so correspondent with that of the Hirudinea, for which Bürger shows so convincingly that the nephridia are mesoblastic, that the view of Bergh would seem to be correct. Consequently Goodrich (1895) in his summary of the literature on this subject would seem to have misunderstood the facts of the case. We may at least conclude, that in light of the evidence at hand all the inner portion of the nephridium is mesoblastic, and only its distal outer termination comes from the ectoblast.

Remarkable postembryonic changes have been described by Rosa (1903*a*) for *Lumbricus*. In a newly hatched individual two canals extend through the whole trunk and join posteriorly into an ampulla that opens dorsally into the intestine (for which reason the describer compares it with the nephridia of Rotatoria). From each of these canals tubes branch off segmentally and connect with the nephridia of the corresponding segments, while the nephridia still lack nephridiopores; later in each segment a diverticulum grows out from each canal and opens on the surface in the position wherein the adult the nephridiopore lies, while in each segment the main canals swell into a pair of vesicles; in the adult these longitudinal canals have disappeared, probably by segmenting into segmental excretory vesicles and nephridiopores.

Development of the Plectonephridia.—In *Megascolides* each segment has one pair of nephridial anlages, each consisting of a preseptal cell and a postseptal cord; so far the development is like that of the meganephridia; then the postseptal cord originates many loops and by a rupture of their connecting bridges the micronephridia result; the longitudinal canals connecting the latter arise later and are therefore secondary (Vejdovský, 1892*b*). In *Mahbenus* Bourne (1894) described an essentially similar process: that the funnels degenerate, that the loops form secondary and the latter tertiary branches, until each segment comes to contain about fifty micronephridia. These observations indicate clearly that the plectonephric condition is a modification of the primary macronephric by a subdivision of originally single organs. This is the position taken by Vejdovský, Bourne and Beddard (1892) which is contrary to the hypothesis of Benham (1890, 1891*a*), Spencer (1889) and Beddard (1891) that the plectonephric condition is primitive and comparable with that of the Plathelminths. Micronephridia lack nephrostomes because they are division products of the loops only, and not of the funnels. Therefore Vejdovský is probably correct in his conclusion that the micronephridia are homologous with the meganephridia, because both arise from a common anlage, comparable with the embryonic pronephridium of *Rhynchelmis*.

In *Acanthodrilus* deverticula grow out from the intestine, at a region probably anterior to the proctodæum, and join with the plectonephridia of that region of the body; this connection is secondary (Beddard, 1889, 1890, 1892).

Embryonic Nephridia.—For *Rhynchelmis* three sets of embryonic excretory structures have been found by Vejdovský (1892*a*). These are (1) "Schluckzellen," cleavage cells containing canals, which had been previously considered to digest the albumen of the egg; (2) larval pronephridia, "Kopfnieren" placed between the germ band and the ectoblast; and (3) embryonic nephridia, which later change into the definitive nephridia. Bergh (1888) found in *Criodrilus* a pair of tubes closed internally that he called Urnieren, though on account of the lateness of their origin Vejdovský considered they are rather embryonic nephridia. Wilson (1889) described for *Allolobophora* a pair of head kidneys, and Hoffmann (1899) found these opened into the head cavity. In the opinion of Vejdovský the larval nephridia develop either from the Schluckzellen, or else come from mesenchyme of ectoblastic origin. But it is yet by no means decided from what germ layer these kidneys originate.

Genital Ducts.—It was Williams (1858) who first indicated the homology of the genital ducts with nephridia, and he held the excretory function to be secondary. Claparède pointed to the typical absence of nephridia in the genital segments as evidence that the genital ducts are modified nephridia. Then Lankester (1865), reasoning from the condition in the Lumbricids, suggested that genital ducts represent the sole traces of a ventral set of nephridia that must originally have existed together with the dorsal set in all the segments; according to this view the primitive relation would be two pairs of these organs to each segment. This idea was adopted by Benham (1886*a, b*) who maintained that in *Lumbricus, Titanus* and *Pontodrilus* the ventral series of nephridia disappears except those that change into genital organs, and that in *Rhinodrilus, Eudrilus, Anteus, Urochæta* and *Moniligaster* just the opposite condition obtains. But Balfour (1885), as most students after him concluded that one pair of nephridia to a segment is primitive, and that "in the generative segments of the Oligochæta the excretory organs had at first both an excretory and a generative function, and that, as a secondary result of this double function, each of them has become split into two parts, a generative and an excretory." Here it is to be recalled that two pairs of nephridia to a segment is unusual, and that only in the Lumbricidæ do both genital ducts and nephridia occur in the same segment; anatomical relations therefore do not bear out Lankester's theory. With regard to the embryogeny of the genital ducts, Vejdovský (1885) found them to arise independently of the nephridia, though he considered they might be wholly or in part homodynamous with the latter; at least the funnels of the two he considered to have this relation. Similar results were reached by Bergh (1886), Roule (1889) and Beddard (1892). Lehmann (1887) opposed the idea of homodynamy on the grounds: (1) That two pairs of nephridia to a segment is not typical; (2) that in the embryo nephridia develop in the genital segments; and (3) that the genital ducts arise later than the nephridia. Finally there may be mentioned the view of Benham (1904) according to whom the phylogenetic series is as follows: (1) The nephridia acted as genital ducts; then (2) a special cœlomostome became added to the nephridia, forming a nephromixium; finally (3) the cœlomostome formed "its own cœlomo-duct, which may either co-exist in the genital segment with the nephridium (as in most 'terricoline' Oligochætes), or the nephridium . . . disappears from the segment during or before the development of the genital duct (as in 'limicoline' Oligochætes and *Protodrilus*). We have, then, to some extent a parallel series of phenomena analogous to those described with so much care by Goodrich in the Polychæta."

There is much in these relations that is still puzzling. But at least the funnels of both organs seem to be homodynamous since they have an approximately similar mode of growth. In the Lumbricids the two organs of a genital segment might well have arisen, as Balfour intimated, as division products of a common embryonic anlage. And in those species where nephridia are wanting in the genital segments, the genital ducts, as Vejdovský argued, are to be considered as in part at least modifications of the nephridia of such segments.

Chloragogue (*Pericardial Gland*).—This is peritoneal in origin and particularly excretory (Grobben, 1888, Rice, 1902, Rosa, 1903*a*).

Peritoneum and Cœlomic Fluid.—These have been considered excretory by Grobben (1888), who holds that the cœlomic fluid is in great part an excretory product though at the same time it has the functions of blood and lymph.

Other Excretory Organs.—Here are to be reckoned the bacteroidic cells of the connective tissues, the yellow cells of the intestine, and the amœbocytes of the blood (Cuénot, 1897).

19. POLYCHÆTA.

Adult Nephridia.—There is usually one pair to each trunk segment. In the Phyllodocidæ, Glyceridæ and Nephthyidæ their inner ends are closed and the loops are beset with solenocytes, each of which is a cell projecting into the body cavity "containing a deeply-staining rounded or oval nucleus, attached by a sort of neck to the extremity of a thin tube which opens at its opposite end into the lumen of the nephridial canal . . . Working inside the tube and attached at its distal end is a single long flagellum, which passes far down the nephridial canal" (Goodrich, 1900). In the other families the inner end is open to the cœlom, with the exception of *Polygordius* (Hempelmann, 1906) where the first pair is closed. The nephridiopores usually open separately. Each pair of nephridia stands in relation to two segments in Archiannelids, Alciopidæ, Typhloscolecidæ, certain Nereids (Eisig, 1887), Terebelloids and Cirratulidæ (Meyer, 1887), Aphroditidæ (Darboux, 1900) and Disomidæ (Allen, 1904); in the other families, therefore in the majority of species, to only a single segment. Some of the main deviations from this type are the following:

(*a*) In Capitellids each nephridium may have several nephrostomes, there may be several pairs to a segment and they may discharge into the skin and not on the surface of the latter (Eisig, 1887). In *Lanice* and *Ploimia* the fourth segment possesses two pairs (Meyer, 1887).

(*b*) In the Terebelloid *Lanice conchilega* the three anterior pairs of nephridia connect with a pair of longitudinal canals from each of which a single nephridiopore discharges on the surface; while the four following pairs of nephridia open into a longer pair of posterior canals which end blindly at about the sixteenth thoracal segment, and each of which discharges by four nephridiopores. *Ploimia* presents quite similar relations. Meyer (1887) who described these conditions holds it probable that the longitudinal canals are formed secondarily by a meeting and fusion of separate nephridial loops, incipient stages of which are to be noted in other genera. Also in *Owenia* (Gilson, 1894) do the nephridia open into longitudinal canals, that are here described as formed by an infolding of the epidermis.

(*c*) In the Terebelloids an impervious dissepiment separates the anterior from the posterior thoracal cavity; in the former there are no germ cells, and the three pairs of nephridia have small funnels; in the posterior space, which communicates with the abdominal cœlom, occur germ cells, and there the nephridia have large nephrostomes (peritoneal funnels) for the discharge of these cells. In the Cirratulids, Serpulacea and Hermellids only the first pair of nephridia are strictly excretory, and the others serve as genital ducts (Meyer, 1887).

(*d*) In Hermellids and Serpulacea the pair of thoracal nephridia unite dorsally into an unpaired duct that opens near the anterior end of the trunk (Meyer, 1887). And in *Dybowscella* the pair of the "head" has a single medio-dorsal pore (Nusbaum, 1901).

Development of the Definitive Nephridia.—The nephrostome of *Polymnia* (Meyer, 1887) arises as a fold of the peritoneum that grows backward to join the loop; the latter developes independently, simultaneously or a little later, from retroperitoneal tissue (whether mesectoblastic or mesentoblastic was not determined) that is at first solid and later acquires a cavity; the distal excretory duct is probably ectoblastic. In *Psygmobranchus* (Meyer, 1888) there first appears in the unsegmented larva a pair of large cells in the blastocœl, apposed to the ectoblast and separated from the mesoblast, these two cells become placed between the two layers of the first dissepiment and give rise to the tubes, while there evaginates to meet each of them a peritoneal funnel. Meyer holds that all the funnels of Terebelloids must have originally been parts of dissepiments, and with the degeneration of the latter have either become independent organs or else have become grafted upon nephridia. In what is the most detailed account of any polychætous nephridium, Lillie (1905) finds for *Arenicola* that the nephridia arise segmentally and independently, entirely from the somatic layer of the mesoblast; at first they are small tubes with intracellular cavities and a minute opening into the cœlom; "the anterior region of these organs . . . together with a portion of the adjoining septum, constitutes the primitive nephrostome, from which the adult nephrostome is directly derived." The terminal vesicle is also not ectoblastic, but "is formed as a differentiation of the most posterior portion of the primitive nephridium. There is no ectodermal invagination," but the terminal portion comes from a region where mesoblast and ectoblast join, probably from a region that was originally ectoblastic.

The work of Meyer, Fraipont and Woltereck shows that Hatschek (1878) was entirely wrong in deriving the nephridia from a continuous anlage, and in stating the adult nephridia of *Polygordius* arise as branches of longitudinal ducts of larval nephridia.

Larval Nephridia.—There is one pair of these in *Polymnia* (Meyer, 1887), each with a long flagellum placed upon the outer surface of the closed inner end, on which region follows a loop composed of two cells and then an excretory canal with intercellular cavity; these persist until the first definitive nephridia function. In *Psygmobranchus* (Meyer, 1888) there is also one pair, each composed of two cells and probably without internal opening, that open on the ectoblast and do not touch the mesoblast; they belong to the first somite (that just behind the metastomium). Meyer (1887) has figured the larval nephridia of *Nereis* as internally closed canals; Hatschek (1885) finds this structural relation in *Eupomatus,* and holds the nephridia to be mesoblastic. In *Hydroides* the head kidney opens into the proctodæum (Wilson, 1890). Drasche (1884, *Pomatoceros*) held the head kidneys to have funnels, and to be mesoblastic.

The larva about which there has been the most discussion is that of *Polygordius.* For *P. neapolitanus* Hatschek (1878) described the branched head kidney as having open nephrostomes and being joined by longitudinal canals with the trunk nephridia, a condition that has led to manifold comparisons with platodan relations. But Fraipont (1888) and Meyer (1901) found that such longitudinal canals do not exist, and that the inner ends of these tubes do not possess funnels but are beset with slender cells (solenocytes) that project into the blastocoel. Meyer described also a second pair of larval nephridia behind these, which differ from trunk nephridia only in the lack of funnels. Then Woltereck (1905) in disagreement with these writers states that the two-branched first pair of larval nephridia belong to the second somite, are mesenchymatous and degenerate entirely; while the second larval nephridium belongs to the third somite and consists of two parts: (1) A mesenchymatous portion, composed of two "Köpfchenzellen" beset with ciliated tubes, that later degenerates, and (2) a segmental portion, at least in part ectoblastic in origin, that joins with the mesenchymatous part. Woltereck finds this second pair to become the first pair of definitive nephridia that differs from the others in the absence of funnels.

In *Polygordius lacteus* Woltereck (1902) found also two pairs of larval nephridia: (1) Hauptnephridia, close to the epidermis of the ventral hyposphere, beset proximally only with tube-cells; and (2) Seitennephridia, lined with such cells along most of their lengths. In the adult of this species also one of these pairs must persist, since the foremost definitive nephridia lack nephrostomes (Hempelmann, 1906).

The present evidence is that the head kidneys are closed internally, and Meyer accounts for this by the lack of a dissepiment in front of them from which a nephrostome could form. But while Meyer and Woltereck incline to an ectoblastic and mesenchymatous origin, Lillie concludes a mesoblastic. There is no evidence that the adult nephridia are division products of larval ones, but when there is a second pair of larval nephridia it may persist in the adult.

Provisory Nephridia.—Following on the larval nephridia and before the adult one are formed there are in the Capitellids (and so far as is known only here among the Polychæta) provisory nephridia, each of which participates in two segments (Eisig, 1887).

Relation of Genital Ducts and Nephridia.—This question has been so ably reviewed by Goodrich (1895, 1900), and his investigations have contributed so much to its solution, that I need to discuss it only briefly. Williams (1858) held that these organs are homologous, and derived from a common "viscus." Then Cosmovici (1880) concluded that the segmental organs of Annelids are of two kinds: excretory organs (organs of *Bojanus*), and genital ducts, and that the two may be separated or may be united. It is the particular service of Eisig (1887) and Meyer (1887 and later papers) to have demonstrated by their anatomical and embryological studies that the peritoneal funnels, the original genital ducts, are evaginations caudad of dissepiments, and that they may or may not join secondarily with the nephridium proper that develops independently from retroperitoneal tissue.[3] But it is Goodrich who has made the most comprehensive comparative investigation of these relations (1895, 1897, 1898, 1900). He calls the peritoneal funnel (Genitalschlauch) a cœlomoduct, and its opening a cœlomostome; when the latter preserves its original strictly genital function it is a gonostome. According to his terminology, further, a nephridium is an excretory organ with its own inner opening, and the latter is a nephridiostome. The cœlomoducts may open on the surface of the body entirely separate from the nephridia, the primitive condition, and in this case the nephridia are purely excretory and possess small nephridiostomes; or the cœlomostomes may become secondarily grafted upon the nephridia, forming compound nephromixia which are genito-urinary and possess large funnels (cœlomostomes). These relations in the Polychætes he tabulates as follows (1900):

Nephridium closed internally.	Genital funnel distinct, but opening into nephridial canal may be acquired at maturity.	Phyllodocidæ. Glyceridæ. Nephthyidæ.
Nephridium open internally.	Genital funnel with independent external opening.	Capitellidæ. ? Nereidæ (Lycoridea).
	Genital funnel becomes connected with the nephrostome, and loses its primitive opening to the exterior.	Hesionidæ (all?). Syllidæ. Aphroditidæ. Eunicidæ. Spionidæ. Terebellidæ. Sabellidæ. Etc., etc.

Goodrich adduces the various evidence for this conclusion and adds: "Moreover, it must be remembered that the two organs are mutually exclusive; never do we find a separate genital funnel in those forms which possess wide-mouthed excretory organs; and conversely, with the one possible exception of Polygordius, never do we find Polychætes having nephridia with only small true nephro-

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[3] Meyer (1890) has shown that Kleinenberg (1886) was mistaken in deriving the genital ducts from the ectoblast.

stomes without genital funnels."[4] Allen (1904) has demonstrated that in *Pœcilochætus* both kinds of organs occur, nephridia with small nephridiostomes in the anterior somites, and nephromixia with large funnels in the posterior.

Thus the evidence is convincing that cœlomoduct and nephridium are two distinct organs, with originally separate origins and functions, but that the two frequently unite to produce a compound nephromixium.

Mid-gut.—This is excretory in the Polynoidæ (Schimkewitsch, 1884), and so are the intestinal cæca in the Aphroditidæ (Darboux, 1900).

Chloragogue.—Schæppi (1894) found the chloragogue of only the peritoneum, nephridia and intrasinous connective tissue is excretory (contains guanin). In *Arenicola* some of the vessels have cæca whose walls possess chloragogue cells (Willem, 1899). For the chloragogue of peritoneal origin (peritoneal glands) Meyer (1901) uses the term "phagocytic organs."

Eisig (1887) has made the most thorough study of excretion in the Polychætes; he determined that carmine is taken up by the mid-gut, then by the peritoneum, and that the hæmolymph is the vehicle of its transport to the nephridia, blood vessels being absent in the Capitellids; it ultimately reaches also the setal glands and the skin; the skin is not excretory though it becomes the seat of excretory substances, and it is by the accumulation of such material that the skin in necessitated to undergo moults.

20. ECHIURIDA.

Segmental Organs.—These serve mainly if not wholly as genital ducts and in *Bonellia* the male lives within those of the female. *Bonellia* has but a single one, while in *Echiurus* and *Thalassema* there are from one to four pairs. Structurally (Greef, 1879, Spengel, 1880) these are long tubes each with a nephrostome close to a nephridiopore. Nothing seems to be known of their development.

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[4] Hempelmann (1906) has since shown that in *Polygordius* the nephridiostomes are too small for the discharge of the germ cells, and that the latter escape by rupture of the posterior end of the body.

Anal Tubes.—There is one pair of these opening into the most posterior portion of the intestine. On their surfaces there are numerous "Wimpertrichter," and Greef supposed these not to open directly into the cœlom, but Spengel demonstrated that they do make such a direct connection and that their ciliated lining is continuous with the peritoneum. Their function is not ascertained. From their position Spengel concluded them to be ectoblastic, but not to be homodynamous with the segmental organs. But Hatschek (1880) describes them as arising not from the rectum but from the somatic mesoblast of the telson; and according to this account they form first the Wimpertrichter, then later the external pores that lie lateral from the anus.

Larval Nephridia.—These are known only from Hatschek's account (1880) of *Echiurus;* the first origin of these "Kopfnieren" was not determined; each becomes a much branched organ with intracellular cavity, from the surface of which delicate blind capillaries grow out. Torrey (1903) was unable to find larval nephridia in *Thalassema,* and determined that in this form excretion is accomplished by certain mesenchyme cells.

21. MYZOSTOMIDA.

The single pair of nephridia were first recognized as such by Beard (1894), and their structure particularly described by Wheeler (1896) and Stummer-Traunfels (1903). Their relations differ somewhat in different species: they may be separated from each other, or their open and large nephrostomes may be united, their nephridiopores may be separated or united; in one species nephrostomes appear to be absent. In some species they are purely excretory, in others also spermiducal. From their development Wheeler concluded that they originally opened on the surface of the body and not into the cloaca (their usual termination in the adult), because in one species the unpaired excretory duct opens "on the surface of the body through a papilla lying just ventral to the cloacal orifice."[5]

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[5] The segmental sacs (suckers) supposed by Nansen (1885) to be nephric, have been shown by Wheeler to be probably sensory.

22. ENTEROPNEUSTA.

Nephridia.—There is a left canal (or a right and left) connecting the cœlom of the proboscis with the exterior, a pair of similar canals in the collar region, and in *Spengelia* (Willey, 1899) rudimentary pores along the whole trunk. Spengel (1893) considered them to take in water from without and to subserve locomotion; Willey regarded them as having lost their former excretory function, while Bateson (1884) showed by carmine injection that the collar pores are excretory.

An ectoblastic origin of these structures was the result of the study of Spengel and Morgan (1894). But Dawydoff (1907), examining those of the proboscis in the process of regeneration, found that they develop from a peritoneal evagination that connects with an ectoblastic ingrowth, and from this concluded that they are true nephridia—a view previously reached by Schimkewitsch (1888).

The genital ducts seem to bear no relation to nephridia, and the larva (tornaria) lacks special excretory organs.

Glomerulus.—A vascular structure connected with the pericardium, considered the only excretory organ in the adult (Willey, 1899); I have not seen the original description and consequently am unable to add further details.

23. MOLLUSCA.

Adult Nephridia.—I have not attempted to labor through the compendious literature on the anatomy of these organs, but shall simply give a brief summary drawn mainly from the excellent treatment by Hescheler (1900). These are essentially similar and homologous throughout the group, and consist typically of a pair of sacs which communicate internally by open nephrostomes (renopericardial apertures) with the cœlom (pericardial cavity), and externally by nephridiopores with the mantle cavity. They are paired in all the groups except the Gasteropods, and among the latter in most of the diotocardial prosobranchs; among living forms there is more than one pair only in *Nautilus*. They may be simple tubes, or may be twisted or excessively ramose. Functionally they may be exclusively excretory, the usual condition, or mainly genital (*Solenogastra*), or genito-urinary.

Development of the Adult Nephridia.—According to one view the glandular portion of the nephridium arises as a peritoneal funnel, an evagination of the pericardium, this joining later with an ectoblastic ingrowth, the duct or ureter; in support of this view is the work of Rabl (1879, *Planorbis*), Erlanger (1891*a, Paludina*), Bütschli (1877, *Paludina*), Salensky (1885, *Vermetus*), Schimkewitsch (1888, *Limax*), Drummond (1902, *Paludina*), Ahting (1901, Pelecypods), Pelseneer (1901, *Helix*), and Stauffacher (1898, *Cyclas*). That these organs are wholly mesoblastic is the opinion of Salensky (1872, *Calyptræa*), Erlanger (1892*b, Bythinia*), Georgevitch (1900, *Aplysia*), and Faussek (1900, *Loligo*). The third view is that they are altogether ectoblastic: Fol (1875, Pteropods), Bobretzky (1877, *Nassa*), Joyeux-Laffuie (1882, *Onchidium*), Sarasin (1882, *Bythinia*), and Meisenheimer (1898, *Limax,* 1901*a, Dreissensia,* 1901*b, Cyclas*).

The first of these views has the greatest support, pointing to the pericardial origin of the funnel and glandular portion, and to ectoblastic origin of some portion of the ureter only. For the third view, wholly ectoblastic origin, it will be noted that the only recent work is that of Meisenheimer. Now almost all the writers conclude a common origin of the glandular portion of the nephridium and the pericardium and Meisenheimer does so likewise, but in opposition to almost all preceding study he regards the pericardium and heart as ectoblastic abstrictions. Meisenheimer must surely be incorrect in interpreting the peritoneum and with it the nephridium as ectoblastic, *i. e.,* he must have defined the germ layers quite differently from other embryologists, since the pericardial cavity is justly considered cœlomic yet in no other animal group is the cœlom regarded as lined by ectoblast.

These definitive nephridia seem to arise independently of the larval ones, save that Rho (1888) and Mazzarelli (1892, 1898) state that the mesoblastic anal kidneys of opisthobranch larvæ become transformed into the adult ones.

Genital Ducts.—" Relations between the nephridial and genital system, similar to those in the Worms, exist in the Solenogastrids where the nephridia function as discharge ducts for the genital products. . . . And again in some Lamellibranchs, Diotocardians and the Scaphopods there exist relations between sex glands and nephridia in that the sex glands open into the nephridia, so that a shorter or longer portion of the latter functions not only as kidney or ureter but also as discharge duct for the genital products' (Hescheler, 1900). In those prosobranchs with only one adult nephridium, Drummond (1902) has shown for *Paludina,* and after a full discussion of the literature, that the right nephridium of the embryo persists as the left one of the adult, in agreement with Erlanger, but contrary to his results she finds the left nephridium of the embryo does not disappear but becomes the genital duct.

Larval Nephridia.—These are known only in Gasteropods and Pelecypods (Lamellibranchs), and it will be most convenient to treat separately the groups in which they occur.

(*a*) *Prosobranch Gasteropods.*—Two kinds of these have been described. (1) External nephridia (Aussennieren, excretory cells). These are ectoblastic, unicellular or multicellular organs, usually projecting from the surface of the body just behind the velum; there is one pair of them, and their cavity communicates with the blastocœl; sometimes they have an opening to the exterior. They have been described most carefully for *Crepidula* (Conklin, 1897) and *Fasciolaria* (Glaser, 1905), also for *Nassa, Natica, Fusus* (Bobretzky, 1877), *Paludina* and *Bythinia* (Sarasin, 1882, who calls them "ansæ"), *Fasciolaria* and *Fulgur* (McMurrich, 1886), *Fissurella* (Boutan, 1885), and *Capulus* (Erlanger, 1892*a*). Glaser has demonstrated that they are first digestive, later serve as reservoirs for waste products, and subsequently fall off from the surface of the larva; Sarasin and McMurrich supposed they were originally parts of the preoral velum, and that with excretory specialization they separated off from it; but Conklin and Glaser show that they arise independently of and before the velum. As "secondary outer kidneys" Glaser has described certain excretory cells placed in the velum and the head vesicle.

(2) The second kind of larval excretory organs of the prosobranchs are mesoblastic. These arise from a mesoblastic anlage that is at first solid, while more or less of the duct is ectoblastic;

they are ciliated with exterior apertures. These have been found in *Bythinia* and *Paludina* (Bütschli, 1877, Erlanger, 1891*a*, 1892*b*).

(*b*) *Opisthobranch Gasteropods.*—Here there are distinguished nephrocysts and anal kidneys. The nephrocysts were discovered and named by Trinchese (1881) for *Ercolania, Amphorina, Bergia* and *Doto;* and were described also by Mazzarelli (1892) for *Aplysia* and by Casteel (1904) for *Fiona*. These are rounded bodies lying anterior to the anus in the blastocœl, without external ducts; nothing positive is known of their origin, and Trinchese supposes them mesoblastic simply from their position. They may occur in the same embryo together with the following organs. The anal kidneys were first interpreted as excretory by Langerhans (1873, *Doris* and *Acera*). They are a pair of single cells, or groups of cells, that originate near the anus but may migrate further forward. Trinchese (1881) and Guiart (1901) derived them from the mesoblast, and so also did Mazzarelli (*Aplysia,* 1892, 1898) who ascribed the occasional unpaired condition to the fusion of a pair. But Lacaze-Duthiers and Pruvot (1887) described them as ectoblastic, and this conclusion was reached also in the careful studies of Heymons (1893, *Umbrella*) and Casteel (1904, *Fiona*). Casteel's work is the most thorough on any opisthobranch, and he states: "There is no point regarding the cytogeny of *Fiona* of which I am more certain than that the group of cells constituting the anal kidney is of ectodermal origin."

(*c*) *Pulmonate Gasteropods.*—Here again there are two kinds of larval kidneys. The external kidneys (äussere Nieren) occur one on either side of the body, each a projecting group of vacuolated cells forming part of the ectoblastic velum. These were discovered by Bütschli (1877), and have been described by Fol (1880) and Rabl (1879) for *Planorbis*. Much more attention has been given to the head kidneys (Urnieren). The most detailed description of these in their perfected condition is that of Meisenheimer (1898, 1899): in the Basommatophora (*Ancylus, Physa, Planorbis. Limnæa*) these are much alike, each consisting of but four cells with intracellular cavity, the innermost of which closes the canal against the blastocœl and bears a ciliary flame. In the Stylommatophora (*Limax, Succinea, Helix, Arion*) the cells are much more numerous and the inner end is composed of a number of large amœboid cells all of which have long cilia; for a while the inner end may be open (as described by Rabl, 1879, and Erlanger, 1894) since the cells there may become loosened from their epithelial connection, but later this end becomes completely closed even though at places by a very thin membrane. These are the most complicated larval nephridia found in Gasteropods; they subsequently degenerate completely. As to the development of these head kidneys: Rabl (1879) and Holmes (1900) considered them mesoblastic; Erlanger (1893) interpreted them as mainly mesoblastic with a portion of the duct ectoblastic, and Pelseneer (1901) stated that the large distal portion is ectoblastic. But Fol (1880), Wolfson (1880) and Meisenheimer (1898) concluded that they are entirely ectoblastic; the last named investigator speaks of them as arising as paired tubular invaginations at the level of the proctodæum.

(*d*) *Pelecypods* (*Lamellibranchs*).—In *Teredo* there is a pair of ciliated Urnieren in the young larva (Hatschek, 1880). Only the left one is developed in *Cyclas,* and opens externally in the region of the head vesicle; it consists of three highly complex cells with intracellular cavity, the innermost branched cell closing it from the blastocœl (Stauffacher, 1898). In *Dreissensia* each of the larval kidneys consists of three cells, the innermost provided with a ciliary flame and closing the canal, the next forming the tube, and the third constituting a duct connecting with the surface (Meisenheimer, 1901*a*). With regard to the embryogeny, Hatschek described these organs as appearing first at the anterior ends of the mesoblastic bands, at first with no connection with the ectoblast, and concluded that the nephridium of each side "is probably derived from only one or a few mesoderm cells"; Stauffacher held that in *Cyclas* only the innermost cells is mesoblastic and the others ectoblastic; while Meisenheimer (*Dreissensia,* 1901*a, Cyclas,* 1901*b*) described them as arising conjointly with the heart and pericardium from the ectoblast.

Homologies of the Larval Nephridia.—Salensky (1872) and Bobretzky (1877) homologized the outer kidneys of prosobranchs with the Urnieren of Pulmonates. Bütschli (1877) suggested that the Urnieren of *Paludina* are possibly homologous with those of the pulmonates, but that there is no homology between the outer kidneys of these groups. Rabl (1879) concluded that the outer kidneys of *Planorbis* are probably comparable with the outer kidneys of freshwater prosobranchs, but not with the Urnieren. Fol (1880) maintained that the outer kidneys of Pulmonates are homologous with the Urnieren of prosobranchs. Erlanger (1893) regarded all the larval nephridia as homologous with each other and probably also with the head kidneys of Annelids, and distinguished the following kinds: (1) Outer ectoblastic kidneys (marine prosobranchs); (2) inner mesoblastic, and these either (*a*) purely mesoblactic (opisthobranchs), or (*b*) mesoblastic with the canal at least in part ectoblastic (pulmonates, pelecypods, freshwater prosobranchs). Mazzarelli (1904) considered the Urnieren of pelecypods, pulmonates and freshwater prosobranchs to be homologous, but the external nephridia of marine prosobranchs to be different structures; and the nephrocysts of opisthobranchs to be organs that have secondarily lost their ducts and that correspond with the excretory cells of the Urnieren of other Mollusks. Finally Glaser (1905) has given a good review of the question, and maintains there are at least three distinct and dyshomologous larval excretory organs (1) Urnieren, mesectoblastic structures of prosobranchs and pulmonates; (2) Aussennieren, modified ectoblastic cells of prosobranchs and pulmonates; and (3) excretion cells, those of *Umbrella* placed near the anus; the Urnieren are further of two kinds because some of them appear to be wholly ectoblastic.

There is so much confusion of opinion with regard to the development of even the same kind of excretory organ in the same species, that I fully agree with Casteel (1904) "that much more work must be done upon these organs of molluscan larvæ before we are ready to come to definite conclusions regarding their mutual relations and homologies, if such exist." There are certainly two distinct kinds that may occur at the same stage in the same species, and that on account of their differences in position, structure and origin are not homodynamous, and these are: (1) Projecting vesicles, wholly ectoblastic, forming part of or placed near to the velum; and (2) vesicular or tubular organs placed below the ectoblast and behind the preceding, which in most cases appear to be in part mesoblastic. All those of the first kind may well be homologous, but those of the second kind are more probably heterogeneous structures.

Other Excretory Organs.—According to Cuénot (1899) the following structures are excretory: in the Amphineura and Scaphopoda connective tissue cells; in prosobranch and opisthobranch Gasteropoda similar cells as well as cells of the liver; in the Pelecypoda pericardial glands; and in the Cephalopoda phagocytes and the gill-hearts.

24. Tardigrada (Arctiscoidea.)

A pair of glands opening into the rectum were supposed by Plate (1888) to be excretory, and he compared them with the Malpighian vessels of the Acarina. But neither he nor Basse (1905), who has furnished a fuller description, were able to find excretory products in these organs. Nothing is known of their development.

25. Pycnogonida (Pantopoda).

Dohrn (1881) has described problematical "Excretionsorgane" within the cavity (blastocœl) of the fourth or fifth joint of the second extremity, or the third or fourth joint of the third; each has an external opening placed upon a small tubercle; in genera where the named extremities are absent, these organs are found in the wall of the body at points opposite the missing extremities. These organs lie in extremities that lack reproductive organs, and for that reason Dohrn suggested they may have some homodynamic relation to the latter.

Kowalevsky (1892) found by injections of acid fuchsine that the stain is taken up by small hypodermal glands placed in *Phoxichilus* on the borders of the three anterior segments and on the bases of extremities fourth to seventh, and in *Pallene* and *Ammothea* in the lateral processes of trunk segments and in the first joints of the extremities.

26. Crustacea.

Shell Glands (Maxillary Glands).—These have been described for the Phyllopoda (Leydig, 1860, Weismann, 1874, Claus, 1875, Dohrn, 1870, Nowikoff, 1905), Copepoda (Claus, 1877, Nettovich, 1900), Isopoda (Vejdovský, 1901; and Nemec, 1896, who states that in *Ligidium* they are modified into salivary glands), Cirripedia, (Bruntz, 1903, Berndt, 1903; in *Balanus* they communicate with the cœlom only in the cypris-stage according to Gruvel, 1894), Stomatopoda (Bruntz, 1903), and freshwater Ostracoda (Claus, 1895, Daday, 1895). These open at or near the base of the second maxillæ, each has a closed enlarged end sac lined by an excretory epithelium, and they are placed in the shell duplicature except in *Leptodora* where the greater portion of the organ lies in the thorax. According to Richard (1892) their ducts are longest in freshwater and shortest in brackish water species. In freshwater Cladócera (*Simocephalus*) I have found that the end sac takes up injected carmine at the end of a few hours.

Antennal Glands.—These have been described for the larvæ (but not adults) of Copepoda and Phyllopoda (Grobben, 1881), for Amphipods (Grobben, 1881, Bonnier, 1891, Bruntz, 1903, Vejdovský, 1901, Della Valle, 1893), Schizopoda (Grobben, 1881, Bruntz, 1903), Ostracoda (Claus, 1890, 1895), Cirripedia where they are modified into cement glands but may still continue excretory (Koehler, 1890), Isopoda (in *Asellus* where they are degenerate, Nemec, 1896), and Decapoda (Marchal, 1892, Waite, 1889). The antennal glands are essentially similar to the maxillary. Both have closed end sacs, are without cilia, and both (Vejdovský, 1901) possess at the junction of the gland and duct a narrow "Trichter" composed of a few large cells with a peripheral muscular sphincter.

Development of the Preceding Organs.—According to the earlier observers (Reichenbach, 1886, Ischikawa, 1885) the shell and antennal glands are ectoblastic, but other studies (Kingsley, 1889, Waite, 1899, Grobben, 1879, Lebedinsky, 1891) show that each arises as a reduced cœlomic sac (or portion of one) connecting with an ectoblastic duct. The end sac of the adult thus corresponds to the cœlomic sac of the embryo.

Maxillipedal Glands.—In *Diaptomus* there is a pair of these opening at the basis of the first maxillipeds; their structure is like that of the preceding glands (Richard, 1892). It is probable that some of the glands described as maxillary are really maxillipedal.

Coxal Glands.—In *Gammarus* (Della Valle, 1893) there are small groups of gland cells, that take up carmine, placed at the bases of the maxillipeds, thoracic and abdominal extremities. Similar appear to be the "Segmentalorgane" of the Ostracoda (G. W. Müller, 1894), which in *Paradoxostoma* lie above each leg pair, and in *Bairdia* above the first pair; and the glands opening on the maxillipeds of Cyprids (Claus, 1890).

Genital Ducts.—The first origin of these seems to have been little investigated, but Pedaschenko (1899) finds them to arise from a proximal mesoblastic and a distal ectoblastic portion.

Homologies of the Preceding Organs.—The maxillary, antennal and maxillipedal glands are probably homodynamous, and seem to differ only in antero-posterior position. Sometimes they occur at the same time in the same individual, or (as in Phyllopods and Copepods) the antennal gland is the larval and the shell gland the adult excretory organ. Sometimes both antennal and shell glands are absent in the adult, as in some Copepoda (Nemec, 1896). Waite (1899) has discussed these homologies at some length, and resumes: "The nephridium of Annelids is *probably* represented in Crustacea in the second (antennal) segment by the antennal gland of Malacostraca; in the fifth (second maxillary) segment by the shell gland of Entomostraca and some Malacostraca; in the sixth (first maxillipedal) segment of *some* Malacostraca by the 'Segmentalorgan' of Lebendinski; it is *possibly* represented in the fourth (first maxillary) segment by the excretory organ described by Boutchinsky, and in the sixth to thirteenth (maxillipedal and pareiopodal) segments in part by the branchial glands, and in part (in the eleventh and thirteenth segments) by the genital ducts."

Nephrocytes.—Bruntz (1903) has found these excretory cells to be distributed as follows: they are absent in the Cladocera; there is one cephalic pair in the Isopoda, Amphipoda and Cirripedia; up to eight pairs placed in the thorax in the Schizopoda, Decapoda (in the gills), and Copepoda parasitica (diffuse); from one to eight pairs in the abdomen in the Isopoda and Stomatopoda (in the legs); and eleven pairs in the thorax and abdomen in the Amphipoda.

Other Excretory Organs.—As such have been described the ferment cells of the liver of Decapoda, Amphipoda and Isopoda, and the mid-gut cæca of Amphipoda (Bruntz, 1903); the mantle in the Cirripedia (Gruvel, 1894); and connective tissue cells of Copepoda when the antennal and maxillary glands are lacking (Nemec, 1896).

27. ONYCHOPHORA (PROTRACHEATA).

Nephridia.—According to the observations of Balfour (1883) and subsequent investigators, one pair of nephridia occurs in each trunk somite, *i. e.,* one pair to each pair of legs, except in the penultimate or antepenultimate segment. Each opens ventrally at the basis of a leg, and consists of an outermost excretory bladder, a loop and a nephrostome that opens into the cœlom; but the portion of the cœlom that has such a connection is, as in the case of the antennal and maxillary glands of the Crustacea, completely abstricted from the remainder of the cœlom and with excretory function, therefore each such cœlomic sac may rightly be considered a closed inner end sac of the nephridium. This is in agreement with the facts of the embryogeny, as detailed by Sedgwick (1885–8) and Evans (1901), according to whom each right and left cœlomic sac pinches into a dorsal and a ventral portion, and the latter portion sends an outgrowth reaching to and opening at the leg.

The salivary glands and genital ducts develop like the nephridia and represent them in segments where they are lacking, are accordingly homodynamous with them (Sedgwick); and the receptaculum ovorum is homodynamous with an end sac of a nephridium (Evans).

Anal Glands.—These also have been considered homologous with nephridia by v. Kennel (1885). But Purcell (1900) has indicated that the so-called "accessory glands" of the postgenital segments may rather be dyshomologous; that while those (anal glands) of the American *Peripatus* are nephridia, those of other genera are probably ectoblastic crural glands.

Nephrocytes.—There are medio-dorsal bands of these, also masses of them near the bases of the legs (Bruntz, 1903).

28. INSECTA.

Malpighian Vessels.—These are absent in Japyx (Grassi, 1888) and also in the Collembola where Folsom and Welles (1906) found that the whole ventriculus is excretory and periodically moults its epithelium; they are not, as generally supposed, absent in the Aphidæ, for Witlaczil (1882) has shown that the so-called pseudovitellus represents them. In all other Insects these vessels are present, and are usually delicate, cylindrical tubes, rarely varicose or ramose, with their inner ends closed and the distal ends joining with the intestine usually at the junction of the mid-gut and proctodæum, and they may insert there singly or by one or several common ducts. In some cases there are two different kinds in the same species. Their number is often constant for a group as may be seen from the following summaries taken from the observations of Dufour (1833, 1841, 1851): in the Diptera there are usually four, rarely five (*Culex*), and never more than four in the Hemiptera; there are generally less than eight in the Coleoptera; six in Phryganids, Termes, Megaloptera (*Corydalis, Sialis*), *Panorpa,* eight in *Hemerobia* and *Myrmeleo;* they are much more numerous in the Orthoptera, Hymenoptera, Libellulidæ and Ephemeridæ.[6]

While Dufour called them "organes hepatiques ou biliaires," subsequent work has proved conclusively that they are the main excretory organs.

According to the majority of investigators they arise as evaginations of the ectoblastic proctodæum, and only in some Hymenoptera do they first appear as ectoblastic evaginations at the posterior end before the proctodæum forms. The largest number known in any embryo is ten (*Melanoplus,* Packard), which seems to be the single case not in agreement with Wheeler's conclusion (1893*a*) that no more than six occur in embryos. Wheeler concludes that six is the primitive number, while others have reasoned this to be four. Only in the Termites are they more numerous in the larvæ than in the adults.

Homologies of the Malpighian Vessels.—These have been compared specially with the sericteries and tracheæ and more generally with nephridia of the annelidan type; and it is most convenient to treat these relations at this place. Bütschli (1870) showed that the sericteries and Malpighian vessels develop like the tracheæ, re-

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[6] A good review of their numerical and other relations is given by Packard (1898). In the Thysanura (except *Japyx*) their number was found by Grassi (1888) to vary from eight to sixteen.

garded the sericteries and tracheæ as homologous, but questioned whether the Malpighian vessels are related to them. Then, following Semper's (1874) suggestion that the tracheæ are metamorphosed segmental organs, Mayer (1875) went further in concluding that the tracheæ, sericteries and Malpighian vessels are homodynamous and all homologous with nephridia of Annelids. Grassi (1885) has in the main supported Mayer, in reasoning that the Malpighian vessels, sericteries, the two transitory invaginations on the head and the homodynamous tracheæ are all probably excretory in the larva; and (1888) supports the idea of the homology of Malpighian vessels with tracheæ on the ground that the former occur in segments where the latter are lacking and are most abundant when the latter are least numerous. But several strong objections have been made to these comparisons, and especially by those who have studied the embryogeny more in detail. Thus Hatschek (1877*b*) has argued against the homology of the sericteries and salivary glands with the tracheæ, that in the segments where the former occur tracheal invaginations are formed independently of them. Then Palmén (1877) concluded that the Malpighian vessels, developing from the proctodæum, were originally hypodermal glands that have come to group themselves around the inner end of the proctodæum and that their number is "in no way dependent upon the number of particular body segments"; while against the homology of the tracheæ with nephridia, he adducted the case of their coincident segmental occurrence in *Peripatus*. Wheeler also (1893*a*) judged that if the Malpighian vessels are homologous with nephridia they can be only with the ectoblastic portion of the latter; and that they are not homodynamous with tracheæ, but rather with the mass of œnocytes that represent the ectoblastic remains of nephridia. Heymons (1896) also concluded that the Malpighian vessels are not to be compared with nephridia, that they are only local evaginations of the hind-gut.

The evidence is that the Malpighian vessels are certainly not homologous with annelidan nephridia, because they are strictly ectoblastic and are not segmental. Their resemblance to the sericteries and tracheæ is only a very general one in that all of these are ectoblastic invaginations, so that at the most we must conclude, with Palmén, that while these may all have had an essentially similar beginning no one of them has been derived from the others. The Malpighian vessels may well have been hypodermal glands that have invaginated with the proctodæum, and for this speaks their independent origin in the embryos of some Hymenoptera. In this connection it is interesting to note the conditions in the larvæ of Phryganids, as described by Henseval (1896): here there are three pairs of ventro-median glands (glands of Gilson); and Henseval regards the Malpighian vessels as homologous glands of the last segment, and the proctodæum as their unpaired portion that has secondarily joined with the mid-gut. If we omit this explanation of the proctodæum as being problematical, the comparison of Malpighian vessels with segmental glands placed anteriorly on the hypodermis might well hold.[7]

Homologues of Nephridia.—Here there are in the first instance the genital ducts, that develop as cœlomic evaginations (Wheeler, 1893, Nassonow, 1886); Wheeler has shown that all the abdominal cœlomic sacs develop such peritoneal funnels, but that only those of one particular somite reach the exterior and become functional genital ducts. He also (1893*a*) holds that the œnocytes represent ectoblastic remains of nephridia. The prothoracic gland of Dicranura has been considered homologous (Latter, 1897). Nassonow (1886) has concluded a like relation for the head glands of *Campodea,* all salivary glands, the maxillary glands of *Lepisma,* and the extensible vesicles of the Thysanura; but Oudemans (1887) and Haase (1889) combat this view and regard the extensible glands at least as not nephridial but as respiratory skin glands. Wheeler (1893*a*) considers the fat-body to represent mesoblastic remains of nephridia; some of its cells are proved to be excretory (Wheeler, Cuénot, 1895, Bruntz, 1903), and Anglas (1901) suggests that such cells compose an "accumulating kidney" that functions during the substitution of Malpighian vessels in the metamorphosis.

Nephrocytes.—According to Bruntz (1903) these cells are labial in *Machilis,* and in it as in *Lepisma* are found also on the fat-body; in larval Neuroptera on the wing muscles; in *Ephemera*

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[7] Other ectoblastic glands regarded as excretory are the segmental globiform glands of *Ocypus* (Georgevitch, 1898).

on the fat-body; in the Hymenoptera, Hemiptera and Coleoptera on the pericardium; in the Lepidoptera usually dorsal in the abdomen; in the Diptera along the heart. The pericardial cells of Cuénot (1895) are perhaps to be reckoned with these.

29. DIPLOPODA.

Malpighian Vessels.—One pair proved to be excretory by Kowalevsky (1896) and Bruntz (1903).

Homologues of Nephridia.—Here are to be placed the genital ducts, that develop like those of *Peripatus* (Heathcote, 1888); and probably the salivary glands that are mesoblastic in origin (Heathcote), and which on account of their closed end sacs are named "rein labial" by Bruntz.

Fat-body and nephrocytes have been shown to be excretory (Bruntz).[8]

30. CHILOPODA.

Malpighian Vessels.—There is one pair of these in all genera (Verhœff, 1902), and they develop as outgrowths from the proctodæum (Sograf, 1883, Heymons, 1901).

Homologues of Nephridia.—The genital ducts are mesoblastic and to be compared with nephridia (Heymons); and Herbst (1891) has described for *Lithobius* a pair of glands with thin-walled end sacs opening behind the second maxillæ, and has suggested that these may be modified nephridia. The salivary glands are ectoblastic and not to be compared with nephridia (Heymons, 1898).

31. SYMPHYLA (SCOLOPENDRELLA).

There is one pair of Malpighian tubules; the ventral sacs are simply respiratory skin glands (Haase, 1889).

32. PAUROPODA.

Malpighian Vessels.—There is one pair of these in *Eurypauropus* but apparently only in the female (Kenyon, 1895). In *Pauropus* they are absent (Schmidt, 1895), and in this genus there are groups of cells in the fat-body that may be excretory (Kenyon).

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[8] Haase (1889) has demonstrated that the ventral sacs are neither excretory in function nor nephridial in origin.

33. XIPHOSURA (LIMULUS).

Coxal Glands.—A very thorough account has been given by Patten and Hazen (1900). The adult gland consists of four nephric lobes at the bases of the second, third, fourth and fifth legs, respectively, and these are connected medially by a stolon of collective tubules; the duct lies dorso-lateral from the latter, is much convoluted and opens at the basis of the fifth leg. The duct arises from a plate of cells of the somatic mesoblast of the fifth somite, this plate invaginating to produce a funnel opening into a thin-walled end sac that represents the fifth cœlomic sac; the distal end of the duct is formed by an ectoblastic invagination. Outgrowths of the end sac finally unite with cell chains of adjacent nephric lobes. In each of the six thoracic somites a mass of nephric cells arises independently of the duct from the somatic mesoblast, and these masses, of which the first and sixth ultimately disappear, form the nephric lobes; offshoots from the four persisting masses produce the canals of the stolon. Thus there are in the embryo six pairs of coxal glands, but only four of them persist in the adult.

The *genital ducts* arise as deverticula of the opercular mesoblastic sacs, and are to be compared with nephridia (Patten and Hazen).

34. ARACHNIDA.

(1) *Araneida.*

Malpighian Vessels.—These are excessively dendritic and their delicate end branches form a fine felt-work around the liver lobes; by a pair of main ducts these open into the intestine just anterior to the rectal vesicle. They have been proved to be excretory (Marchal, 1889, Bruntz, 1903). Balfour (1880) and Morin (1888) described them as arising from the ectoblastic proctodæum; but with the exception of Kishinouye (1890, 1894) who derived them from the mesoblast, the other embryologists (Loman, 1887, Schimkewitsch, 1897) find that they develop from the entoblastic mid-gut. Locy (1886) described them as coming from the prestercoral tube, but though the latter is probably entoblastic its origin was not definitely settled. Renewed investigation is needed on this question, but the entoblastic origin seems to be best authenticated.

Coxal Glands.—Evidently these are not functional but are degenerate in the adult; Bruntz (1903) has proved they are excretory. In the young of *Atypus* there is a pair of these opening on the third coxæ (Sturany, 1891), but the duct is lacking in the adult (Sturany, Bertkau, 1885). In the young of *Mygale* Loman (1888) states it is degenerate, while Pelseneer (1885) finds no ducts but on each side of the body a four-lobed gland corresponding to the four extremities of the thorax. Sturany and Hansen and Sörensen (1904) state that in the Tetrapneumones it opens behind the fifth extremity (third leg) and in the Dipneumones behind the third (first leg). Kishinouye (1890) maintained that these organs arise from the ectoblast, though he showed that the anlage opens by a funnel into the cœlom.

Genital Ducts.—Purcell (1895) has shown that these arise as evaginations of the cœlomic sacs; "the similarity of their development with that of the coxal glands in Arachnids generally indicates their nephridial origin."

Hind-gut.—This is said to serve as an excretory organ until the Malpighian vessels are developed (Bertkau).[9]

(2) *Scorpionidea.*

Malpighian Vessels.—These are branched, four in number (Dufour, 1854); though generally supposed to have the same function as those of other arachnids they are stated by Bruntz (1889) to be not urinary. They arise from the entoblastic mid-gut (Brauer, 1895).

Homologues of Nephridia.—The genital ducts develop like and are homodynamous with the coxal glands (Brauer, 1895). The latter are in one pair and open behind the fifth extremity (third leg); Bruntz has shown that they have an excretory function. These have each a narrow duct and an enlarged inner end sac. Bernard (1893) held these glands to be ectoblastic, independent of the cœlom, homologues of acicular glands. But the researches of Laurie (1890), Sturany (1891) and Brauer (1895) have demonstrated that they arise each as an outpushing of the somatic mesoblast that

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[9] The spinning glands are ectoblastic, and may be equivalent to crural glands, but are neither excretory nor nephridial.

reaches to and opens upon the skin, then later loses this opening; Brauer found that a series of them arise, in segments third to sixth, inclusive, but that all but those of the fifth segment soon disappear.

(3) *Cyphophthalmidea.*

Malpighian Vessels.—There is one pair of these in *Gibocellum,* opening at the junction of the mid-gut and hind-gut; they are of great size and each is remarkable in having a net-like branching at its middle only (Stecker, 1876).

Coxal Glands.—Sturany (1891) holds what Stecker called "Speicheldrüsen" to be probably coxal glands; there is one pair of them on the sides of the stomach.

(4) *Phalangida.*

There are here no Malpighian vessels, and their absence is due, according to Loman (1888), to the functional persistence of the coxal glands. The latter are organs with an inner closed end sac (Faussek, 1892), that open in the Opiliones laniatores behind the third, and in the Opiliones palpatores and Chelonethi behind the fifth extremity. They develop as mesoblastic outgrowths of the particular extremities in which they are placed (Sturany, 1891, Faussek, 1892).

(5) *Pseudoscorpionidea* (*Chernetidæ*).

Here also there are no Malpighian vessels. The coxal glands are stated to have no exterior openings, to lie at the base of the fifth extremity, and to be of mesoblastic (nephridial) origin (Sturany, 1891). The spinning glands that have two pairs of opening on the chelicera are considered by Bertkau (1888) to be homologous with them.

(6) *Solifugæ* (*Galeodidæ*).

Malpighian Vessels.—These are one pair of branched tubes.

Coxal Glands.—There is one pair placed between the third and fourth coxæ; Bernard (1893) considered the end sacs to be prolongations of the ducts, but his account is not convincing. Loman (1888) has suggested that the poison glands are homologous with them.

(7) *Microthelyphonida* (*Palpigradi*).

There are no Malpighian vessels but the adult excretory organs are the coxal glands, and have been described by Rucker (1901) and Börner (1904). There is one pair of these extending forward from the third abdominal segment to their opening between the second and third legs; the great size of these Börner gives as the explanation for the loss of Malpighian vessels.

(8) *Pedipalpi* (*Thelyphonida*).

Malpighian Vessels.—According to Börner (1904) there is one very ramose pair of these; they develop from the entoblastic stercoral pocket near its posterior end (Laurie, 1894).

Coxal Glands.—These are strongly developed, function in postembryonic life, and their ducts open on the third pair of coxæ (Börner).

(9) *Acarina.*

My account of this group is necessarily very defective because for the most part I have seen only reviews of the literature.

Malpighian Vessels.—These seem to be absent in many species, but a pair of them has been described for *Ixodes* (Wagner, 1894), Gamasidæ (Michael, 1892, Winkler, 1888), *Halarachne* (Kraemer, 1885), and Tyroglyphidæ (Nalepa, 1884, 1885, Haller, 1880). In the nymphs of Gamasids these penetrate deep into each leg. For *Bdella* Karpelles (1893) has described an unpaired excretory organ of entoblastic origin opening into the rectum.

Caudal (*Proctodæal*) *Excretory Organs.*—These are urinary structures opening at the posterior end of the trunk without connection with the mid-gut, and are tubular or saccular, closed internally. These may be present (1) when the intestine is provided with an anus, as in *Hydrodroma* (Schaub, 1888); or (2) when the mid-gut ends blind and has no anus, as in Prostigmata (Thor, 1904), Gamasidæ (Michæl, 1892, 1895), and *Trombidium* (Croneberg, 1879, Henking, 1882). The suggestion was made by Thor that the second type probably represents a rectal bladder with Malpighian vessels that have become separated from the mid-gut. But the first type, that has an opening separate from the anus, cannot have been so formed, but would rather seem to be ectoblastic like the Malpighian vessels in Insects.

Unicellular Glands of the Intestine.—Nalepa (1888) has described for Phytopids three large unicellular glands in connection with the rectum, and supposed they may be excretory.

Coxal Glands.—In *Limnocharis* Thon (1905) found a pair of glands in the region of the second coxæ; in *Eulais* they are most active in the nymphal stage while they degenerate in the adult (by substitution of the proctodæal organ), but in *Limnochares* they function even in late life. Supposed coxal glands have also been described by With (1904) for the Notostigmata, by Sturany (1891) for *Trombidium,* by Winkler (1888) for Gamasidæ, and by Michæl (1883) for Oribatids. The lateral abdominal glands of Gamasids, Tyroglyphids and Oribatids may be homodynamous. The development of these various glands seems to be quite unknown, so that nothing can be said of their homologies.

35. LEPTOCARDII.[10]

The nephridia in *Amphioxus* were discovered by Weiss (1890) and particularly described by Boveri (1892). The latter found them to be segmentally arranged, in about ninety pairs in the branchial region, there being one pair to every two branchial arches. Each nephridium was described by Boveri as a canal with one opening into the ectoblastic atrium, and several into the cœlom (subchordal cavity); inserting into the orifice of each of these nephrostomes, but not into that of the nephridiopore, is a tuft of long Fadenzellen. Goodrich (1902) has reinvestigated these organs, and while he confirmed the preceding account in most particulars, he found that the Fadenzellen are solenocytes, each hollow with a long cilium and each closed from the body cavity, and that there are no open communications of nephridia with the cœlom: "These tubules are situated 'morphologically' outside the cœlom, being covered with cœlomic epithelium; the solenocytes alone push through into the cœlomic cavity." And he concluded "that in their

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[10] The Leptocardii exhibit so many morphological peculiarities that they are to be removed from the group of the Vertebrata; the Craniota by themselves compose a homogeneous assemblage.

segmental arrangement, in their function, and in their histological structure, the excretory organs of *Amphioxus* and the nephridia of *Phyllodoce* are in all essentials identical." In a second communication Boveri (1904) maintained the occurrence of true nephrostomes, and held the solenocytes to be modified peritoneal cells and not to be covered by a peritoneal investment.

Unfortunately nothing is known of the development of these structures.

36. VERTEBRATA (CRANIOTA).

With regard to the excretory organs of this group I shall deal reather summarily, because they have been much more studied than the excretory organs of other animals, and because most of the larger contributions on the subject deal extensively with the literature.

Nephridia.—Good reviews of the embryogeny of these structures have been presented particularly by Rückert (1892), Boveri (1892), Wheeler (1899) and Brauer (1902). There are three kidney systems which occur in the ontogeny in the order of their naming; the pronephros, mesonephros and metanephros. The first two occur in all vertebrates, the third in amniotes only. The pronephros is purely an embryonic structure except in *Bdellostoma, Lepidosteus* and some Teleosts (*e. g., Fierasfer*) in which it functions also in the adult. The mesonephros is the adult kidney of all other anamniotes, and the metanephros of the amniotes. All these organs are paired and segmented.

Pronephros.—This develops in the anterior trunk segments as serial solid thickenings of the somatic mesoblast, each of which secondarily becomes tubular and pushes towards and opens into the cœlom. Their lateral ends unite to form the collecting tubule. The arterial connection is in most cases by a paired glomus, an unsegmented vascular inpushing of the dorsal peritoneum medial from and opposite the nephrostomes. The duct, generally known as the segmental duct, also as the pronephric or Wolffian duct, arises just lateral from the tubules and grows back from them to open into the cloaca; in the Selachii and Mammals, possibly also in *Lepidosteus,* it is ectoblastic and joints secondarily with the tubules; in all other forms it arises from the somatic mesoblast in conjunction with the tubules and like them is at first solid. Some of the more important papers on the development of these structures are the following: for the Amphibia, Fürbringer (1878), Mollier (1890), Field (1891), Semon (1891), and Brauer (1902); for the Cyclostomes, Wheeler (1899), Price (1897); for the Selachii, Balfour (1881), Van Wyhe (1889), Rückert (1888), Rabl (1896); for the Teleostei, Hoffmann (1886), Henneguy (1888), H. V. Wilson (1891), Swæn and Brachet (1901); for the Ganoidei, Parker and Balfour (1882), Beard (1889); for the Reptiles, Hoffmann (1889), Gregory (1900); for Aves, Sedgwick (1881), Balfour (1881), Renson (1883), Felix (1891); and for the Mammals, Spee (1884), Flemming (1886), Kollman (1891), Martin (1888).

Mesonephros.—These tubules develop usually in the segments behind the pronephroi, but there are certain segments that may contain both of them, and they are more numerous and more differentiated that the pronephroi. To understand their origin it is necessary to recall that the cœlom becomes divided into the dorsal myocœls (cavities of the myotomes or somites), the middle nephrocœls, both of these being segmented and paired, and the large unsegmented hypocœl that is imperfectly paired; these relations were established particularly by Van Wyhe. Very early the myocœls pinch off from the nephrocœls, whereby the latter are left as short tubes, the dorso-lateral end of each ending blindly while the ventral opens into the hypocœl. These peritoneal nephrocœls become the mesonephroi and grow laterad to join with and open into the segmental duct, for they develop no duct of their own. The arterial connection is segmental: From the aorta a vessel grows towards each tubule and ends in a capillary glomerulus against the wall of the latter above the nephrostome; the wall of the tubule forms a partial sheath (capsule of Bowman) around the glomerulus, In *Petromyzon* there is a larval as well as a definitive set of these tubules, and there may be several in each segment (Wheeler).

The principal studies on the mesonephros are these: For Selachii, Rückert (1888), Van Wyhe (1889), Rabl (1896); for Teleostei, Felix (1897); for Cyclostomata, Wheeler (1899), Price (1897), Maas (1897); for Amphibia, Semon (1891), Brauer (1902), Hall (1904); for Reptiles, Gregory (1900), Mihalkovics (1885), Wiedersheim (1890); for Aves, Sedgwick (1880), Felix (1891); and for Mammals, Janosik (1887), Martin (1888), H. Meyer (1890).

Metanephros (*Kidney of Amniotes*).—This consists of the duct or ureter, and the kidney proper, both developing behind the mesonephros. The ureter is a dorsal outgrowth from the segmental duct. There are two views concerning the origin of the glandular kidney. According to the first and older of these the kidney tubules arise as evaginations from the anterior end of the ureter (Kölliker, 1861, Waldeyer, 1870). There is much more evidence for the second view, origin independent of the ureter from mesoblastic tissue (Emery, 1883, Hoffmann, 1889, Wiedersheim, 1890). The ureter grows forward into an embryonic cell mass known as the kidney blastema, of somewhat uncertain origin, but possibly homodynamous with the anterior mesonephric anlage (Wiedersheim). According to the description of Emery (1883) the so-called collective tubules of the kidney arise as blind outgrowths of the ureter, and these join with the secretory tubules that arise independently from the kidney blastema. There is still much to be decided concerning the exact method of formation of the kidney, but certainly a considerable portion of it arises independent from the ureter from somatic mesoblast. Each tubule of the metanephros commences proximally with a Malpighian corpuscle, that is, a vascular glomerulus enclosed in a capsule of Bowman, a vascular relation like that of the mesonephroi; metanephric tubules lack nephrostomes or other connections with the cœlom.[11]

Relations of these Nephridial Systems.—That the pronephros and mesonephros are homodynamic is the view of Balfour (1881), Sedgwick (1881), Price (1897) and Brauer (1902). Field (1891) argued that the two are differentiated parts of one ancestral organ, that differ structurally because they develop at different periods. But the majority of investigators hold them to be not homodynamous, and here may be mentioned W. Müller (1875), Fürbringer (1878), Van Wyhe (1889), Rückert (1892), Semon (1891), Rabl (1896), Wheeler (1899), and Maas (1897). If we omit the conditions in the Gymnophiones in which the relations of the pronephros

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[11] Adult mesonephric tubules may still maintain their nephrostomes, or may lose them; cf. Spengel, 1876.

appear strongly modified or at least quite different from those in other groups, then it is highly probable that these two organ systems are not strictly homodynamous. For the pronephroi arise as solid thickenings of the somatic mesoblast, that later become tubular and only secondarily join with the cœlom; and their vascular supply is an unsegmented glomus opposite their nephrostomes. On the other hand the mesonephroi are abstricted portions of the cœlom (nephrocœls), they are from the start peritoneal and in open communication with the cœlom; and the vascular connection of each is a Malpighian corpuscle. The pronephroi are retroperitoneal, the mesonephroi, peritoneal funnels in the main; the former develop in close connection with the segmental duct, while the latter arise much later than it and join it secondarily. In view of these differences pronephros and mesonephros are probably only incompletely homodynamous.

As to the metanephros, its ureter being an outgrowth of the segmental duct is a new structure; while the glandular kidney arises from mesoblast that may represent a late generation of mesonephric tubules. Accordingly, the metanephros can be only in part homodynamous with the mesonephros.

Homologues of Nephridia.—Here are to be placed the genital organs that I will treat very briefly. Particular genital ducts are absent in the Cyclostomes, *Lœmargus* and certain Teleostei; here the genital cells fall into the cœlom and are discharged through peritoneal canals, supposed peritoneal funnels (Weber, 1886), the development of which has not been studied.

In the males of Teleosts and certain other fishes the genital ducts are simply outgrowths of the gonads, while in all other forms the segmental ducts (or portions of them) are urogenital. The vasa efferentia of the testis, the paradidymis and the hydatid of Morgagni are modified mesonephric tubules.

In the females of all forms except most Teleosts and *Lepidosteus,* where the ducts are outgrowths of the gonads, the oviduct (with uterus when present) is distinct from the urinary canal (segmental duct or ureter) and is known as the Müllerian duct. This is paired and arises in the Selachii as a longitudinal abstriction of the segmental duct, but in other forms as a structure independent of the latter, *i. e.,* as a longitudinal peritoneal groove, showing sometimes (Reptiles) traces of segmental origin, that becomes a tube closed from the cœlom except at its anterior end (ostium). These two kinds of Müllerian ducts cannot be homologized, for the first is an abstriction from the segmental duct, while the second arises as a peritoneal infolding and may be compared with an elongated peritoneal funnel or with a series of them. The ovaries differ from testes in lacking vasa efferentia connecting them with the ducts, but other remnants of mesonephric tubules are found in amniotes in form of the epoöphoron and paroöphoron.

Other Excretory Organs.—The liver forms urea, while the sudoriparous glands, respiratory organs and skin aid in the discharge of waste substances.

B. GENERAL COMPARISONS.

I. MAIN TYPES OF EXCRETORY ORGANS.

We use the idea homology to denote that relation between a certain organ of one animal and a certain organ of another, which is dependent upon derivation from a common ancestral organ. In other words, homology denotes community of descent of parts. To elucidate such relations, to demonstrate change of both form and use of parts, is the first object of comparative anatomy; later all such knowledge may be so compounded as to give the general history of phylogeny. When one considers such manifold and diverse organs as those that subserve excretion, difficulties of interpretation that are almost insuperable arise to perplex and bewilder, yet at the same time compel, the attention. Any conclusions with regard to the homologies of these organs must be tentative because our knowledge of them is so very imperfect; in fact for most of the animal groups only the outlines have been made known. Therefore the following attempt to arrange the excretory organs according to their genetic relations should be regarded as only an essay.

The criteria of homology are still a matter of dispute. I have discussed this matter in another place (1906), and will simply state here that similarity of relative position to other parts seems to be the surest criterion, together with general similarity in mode of ontogenetic formation. We shall place first relative position with regard to the outer skin, the blastocœl and cœlom, the intestine and the genital organs. These relations involve genetic connections with the particular germ layers, and a word of discussion may be in place with regard to these. The concept of the essential homology of the primary germ layers has been many times attacked since its formulation by Huxley and Kowalevsky. Yet these objections have been weakened by much of the more recent work. Ectoblast always furnishes nervous elements, entoblast originates digestive and assimilative parts, from the mesoblast come the reproductive cells; these are cardinal distinctions that seem to hold throughout the Metazoa. Therefore it is no valid objection to the idea of the homology of these layers to cite the observations of Chun on Ctenophores, that in the process of gemmation an ectoblastic outpushing gives rise to both ectoblast and entoblast. This observation can rather prove only that such an ectoblastic bud is not purely ectoblastic but mixed in its nature. And when Heymon's studies on Insects, resulting in the completely ectoblastic formation of the whole intestine, are brought up as an objection, it may be answered that the observational distinction of the germ layers in insects is very difficult, and also that these conclusions have not been corroborated by all subsequent examiners. The oft-cited case of the Trematodes, to the effect that the embryo throws off its whole ectoblast, must now be allowed to drop since Goldschmidt has demonstrated that it is not the true ectoblast but only a follicle cell layer that becomes so moulted. For these and other reasons those critics are becoming fewer who maintain that ectoblast is not always homologous with ectoblast, and entoblast with entoblast throughout the Metazoa; and the most painstaking of all embryological work, that on cell-lineage, bears out most strongly the well-founded general homologies of these primary layers. The discussion has shifted rather to the significance of the mesoblast, the existence of which was so stoutly denied by Kleinenberg. This long and wearying discussion has brought out the result, first clearly stated by Meyer, that two kinds of mesoblast are to be sharply distinguished, the primary or mesectoblast, and the secondary or mesentoblast. The probable correctness of this distinction is amply substantiated by the cell-lineagists, and the arguments for it have been well presented by Torrey. The mesectoblast is of ectoblastic origin, it is in part equivalent to the mesenchyme of the Hertwigs; it forms larval and to less extent adult structures, but never gives rise to germ cells. The mesentoblast form adult structures and contains the germ cells. These again are fundamental differences, so that it is no longer sufficient to state a part is mesoblastic, it is necessary to know whether it is mesectoblastic or mesentoblastic. The mesectoblast is in reality an emigrant or delaminant of the ectoblast, it is genetically related with that layer and not with the mesoblast.

Relation of position to, and origin from, these four embryonic layers gives then a primary criterion for deciding the homologies of the excretory organs. And these relations of position involve also place-relations with regard to the primary cavities of the body: The blastocœl, the space between ectoblast and mesoblast; the cœlom, the space lined by mesentoblast; and the gastrocœl, the space lined by entoblast.

Using the relations of position and origin as of primary importance, and anatomical and histological relations as of secondary, we will proceed to arrange the excretory organs in genetic groups. Many of the organs described in the preceding part of this paper could not be entered here on account of the insufficiency of our knowledge concerning them; and some others have to be marked doubtful for the same reason. It is at the best a hazardous undertaking to classify other men's results, and the danger is multiplied when descriptions are imperfect.[12]

(*a*) *Wholly Ectoblastic Excretory Organs, not Opening into the Cœlom and not Serving as Genital Ducts.*

1. Hypodermal skin glands. These are perhaps the most primitive excretory organs, and are of wide distribution. Excretory function of them has been proved for Pycnogonids, Insects, Arachnids, Vertebrates and certain others; but probably most hypodermal glands are rather secretory than excretory.

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[12] Here may be mentioned a generalized embryonic excretory organ, the blastocoel, which Kofoid has shown to have the value of a discharging vesicle and to continue that function up to the gastrula stage; Meisenheimer has accepted Kofoid's conclusions.

2. Evaginated vesicles, open to the blastocœl. Here are to be reckoned the outer nephridia of prosobranch and pulmonate molluscan embryos, and probably the anal kidneys of opisthobranchs. The latter have a method of formation similar to that of the others, but they differ in position.

3. Tubular invaginations terminating blindly in flame cells, with the cavities of at least the capillaries intracellular. Their origin from the ectoblast has been proved only in the case of the Nemertini and Acanthocephala and with some doubt in the Polycladidea. Here are to be placed the definitive nephridia of the Platodes, Nemertini, Gastrotricha, Rotatoria, *Rhodope,* Acanthocephala, and the larval nephridia of *Phoronis;* probably those of the Endoprocta should be placed here (if they are not mesectoblastic), and perhaps those of the Priapulida and the head kidneys of some Molluscan larvæ. This type of excretory organ has been named by Hatschek (1888) protonephridium, though he extended this term to cover also organs of mesectoblastic and even mesentoblastic origin. This is a very natural group of excretory organs, showing great similarity in both structure and development. The only case of a larval or head kidney among them is that of *Phoronis,* yet here this kidney persists into the adult though it later joins with a cœlomostome. Kaiser (1892) is inclined to compare the organs of the Acanthocephala with those of Annelids or even with the anal kidneys of *Bonellia,* but their strictly ectoblastic origin renders this view unlikely; while those of the Acanthocephala open into the genital ducts, so also do those of certain Turbellaria, consequently this relation does not speak against their community.

4. Tubular invaginations with wholly intercellular cavity, without flame cells of cilia. These are the Malpighian vessels of Insects and Chilopods (? and of other Myriopods), the proctodæal organs of the Acarina, and possibly the rectal tubes of the Tardigrada. All of these either open into the proctodæum or upon the surface of the body near the anus; it is probable they secondarily acquired the proctodæal position when the ectoblast invaginated to produce the end-gut. These tubes are usually unbranched, but in some Insects they are dendritic. They differ from type 3 mainly in lacking cilia and in possessing a wholly intercellular cavity; but the

lack of ciliated epithelia is a histological characteristic of the groups that possess them.

(*b*) *Mesectoblastic Organs.*

Here are to placed the following structures:

5. Scattered excretory cells, such as connective tissue elements of the Mollusca, and possibly the bacterioidic cells of the Oligochæta.

6. Closed vesicles, the kidney sacs of Tunicata, and possibly the nephrocysts of nudibranch Mollusca. These seem to act as centers of accumulation of waste substances.

7. Tubes communicating with the exterior, the inner ends blind and terminating with a flame cell or solenocytes. In all probability the larval nephridia (head kidneys) of Oligochæta and Polychæta belong here (in the latter sometimes a portion of the duct is strictly ectoblastic); possibly the nephridia of the Dinophilea fall also into this category, but nothing is known as yet of their development. In their structure these are very similar to the organs of type 3, the protonephridia in the restricted sense, the only difference being that the one come directly from the ectoblast, the others from the mesectoblast.

(*c*) *Organs Wholly or Partially Mesentoblastic.*

These represent the more specialized kinds of excretory organs, correspond in part to the metanephridia of Hatschek, and may be subdivided into the following main types:

8. An ectoblastic invagination joining directly (without participation of retroperitoneal mesentoblast) with a cœlomostome (peritoneal funnel), the involved portion of the cœlom not exclusively excretory. Examples are the adult nephridia of *Phoronis,* and the head and collar pores of the Enteropneusta; homologous with these is the stone canal of the Echinodermata. The present evidence does not allow us to decide whether the segmental organs of the Sipunculida, Ectoprocta, Brachiopoda, Echiurids and Myzostomes belong with this type or with type 11.

9. An ectoblastic invagination joining directly (without participation of retroperitoneal mesentoblast) with a reduced cœlomic sac, the latter being an exclusively excretory end sac. There are

two main kinds of these: (1) The ectoblastic portion very small, and the end sac representing only a portion of the cœlom of a segment, as in the case of the salivary glands, nephridia, and genital ducts of the Protracheata. And (2) the ectoblastic portion relatively larger, the end sac being a whole cœlomic sac, as in the case of the coxal glands of Arachnids, Xiphosura, Crustacea, the salivary glands of Diplopods, and the antennal, maxillary and maxillipedal glands of Crustacea.

10. An ectoblastic tube joining with retroperitoneal mesentoblast, the latter neither joined with a cœlomostome nor serving as a genital duct; the inner end is either quite closed or else has a small opening (nephridiostome) into the cœlom; the cavity is usually intracellular. Here belong the larval nephridia of the Hirudinea, and the definitive nephridia of the Hirudinea, Oligochæta and some Polychæta (Phyllodocidæ, Glyceridæ, Nephthyidæ, Capitellidæ, and perhaps the Nereidæ). Probably the anal kidneys of Echiurids belong here, and perhaps also the nephridia of the Nematoda. In essential agreement with this type is the pronephros of the Vertebrata, which also consists of a retroperitoneal mesentoblastic tube whose inner end opens secondarily into the cœlom (not by a peritoneal funnel) and whose outer end joins with the segmental duct that is of either mesentoblastic or ectoblastic origin. Possibly the nephridia of the Leptocardii are also homologous, as Boveri has suggested, but nothing is known of their development; it will be recalled that Boveri homologized the atrial chamber of the Leptocardii with the segmental duct of the Vertebrata.[13] There is no homology between the segmental duct of Vertebrates and the longitudinal canals of the Polychætes *Lanice* and *Ploimia,* for the latter seem to be formed by a late fusion of the secretory portions of the

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[13] As to the phylogeny of this segmental duct, Balfour considered it to be the foremost modified pronephric tubule, and Field has accepted this view. Haddon (1886) and Beard (1887) suggested that the pronephroi first opened separately into an open ectoblastic groove, that later closed to become the segmental duct. Rückert (1888) also concluded that originally the pronephric tubules opened independently to the exterior, and that they extended through the whole trunk; he maintained that the segmental duct arose by the meeting and fusion of their lateral ends, that is, by a backward growth of collective tubules.

nephridia. Indeed, the segmental duct of Vertebrates appears to have originated in this class.

11. An ectoblastic tube (though this portion may be very small) joining with retroperitoneal entomesoblast, and the latter connecting with a cœlomostome; these are generally either urogenital or homodynamous with genital ducts, and the cavity is usually intercellular. The inner end is widely open at least in the embryo. These correspond to type 10, with the addition of a cœlomostome. In this type fall the nephridia of the Mollusca, and those of most Polychæta. As mentioned above, the segmental organs of the Sipunculida, Ectoprocta, Brachiopoda, Echiurida and Myzostomida probably belong either here or with type 8. Essentially homologous are the mesonephroi, therefore probably also the metanephroi, of the Vertebrates, which consist to great extent of peritoneal funnels. And Boveri has argued that the gonads of the Leptocardii may be homologous with these mesonephroi.

12. Non-tubular peritoneal differentiations of excretory nature. Here are the so-called ciliated funnels of the Holothurians, that are not funnels (cœlomostomes) at all, and the widely represented peritoneal glands (phagocytic organs, chloragogue *in parte*).

13. Non-tubular retroperitoneal mesentoblastic cell masses. With these belong a variety of structures the development of most of which has been little examined, such as the excretophores of the Hirudinea and the fat-body of Insects (the latter perhaps representing, as Wheeler has suggested, the remains of nephridia).

(*d*) *Entoblastic Excretory Organs.*

14. These are relatively few in number and seldom have an exclusively excretory function. In the first place there are tubular evaginations of the mid-gut, as the Malpighian vessels of Arachnida, then the mid-gut cœca of the Polycladidea and Amphipoda and probably of the Arachnida; these are all essentially homologous. The whole mid-gut has been shown to be excretory in the Collembola, *Dinophilus* and the Ectoprocta; it seems to be specially so only when other excretory organs are wanting, and in that case there is either periodical moulting of the lining of the mid-gut

(Collembola), or when this fails there is rapid death of the individual from poisoning of the intestinal tract (Ectoprocta).

2. Homologies of the Preceding Types.

The entoblastic type (14) is *sui generis* and not related to the others. Types 12 (peritoneal glands) and 13 (retroperitoneal differentiations) are so generalized in both structure and function, that it is hardly advisable to attempt to draw homologies between them; and the same holds for types 1 (ectoblastic skin glands), 2 (ectoblastic vesicles), 5 (scattered mesectoblastic cells) and 6 (mesectoblastic vesicles). There remain then for consideration all those distinctly tubular organs, nephridia proper, into the composition of which entoblast does not enter.[14] The earliest and most uniform of these are those of type 3, ectoblastic invaginations terminating in flame cells, which are referable, as argued by Lang, to still simpler skin glands. Type 4, ectoblastic invaginations like 3 but without cilia, are essentially similar; for no one would hesitate to homologize the mid-gut of the Turbellaria and the Insects, though the former is ciliated and the latter is not; therefore one should not object to drawing homology between the water vascular system of the former and the Malpighian vessels of the latter. The lack of cilia is not a characteristic merely of these vessels, it marks all the tissues of the Insects. The only differences between types 3 and 4 is the lack of cilia in the latter, and this is a difference that is of little homological importance, a merely histological character. And essentially similar to both of these is type 7, tubes of mesectoblastic origin; they do not come immediately from the ectoblast, but from tissue of ectoblastic derivation which is but a step removed. These three types, accordingly, 3, 4 and 7 are anatomically and embryologically essentially alike, they are to be considered homologous; they stand in no relation to the cœlom, never conduct the genital prod-

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[14] The term nephridium has been used very variously since its coinage by Lankester (1877). It might be well to limit it in the future to tubular excretory organs not containing entoblast. In the descriptive part of the paper I have discussed special homologies of excretory organs within the same group, such as relations of embryonic to adult nephridia, of meganephridia and plectonephridia, homologies of tracheæ, etc.; these need not be repeated here.

ucts, and contain no mesentoblast. I would propose that Hatschek's (1888) term protonephridium be limited to them.

From such protonephridia the other types of nephridia have probably been derived by the persistence of only the discharge ducts, or portions of them, of the former and by the substitution of mesentoblastic elements for their other portions. The only elements of the protonephridia that have been retained, it should be repeated, are their distal nephridiopores with more or less of the connectant discharge ducts, while the remainder of the protonephridia, all the excretory portion proper, has been replaced by mesentoblastic elements. Accordingly, the two other main kinds of nephridia of which we shall have to speak can be at the most compared only in part with these protonephridia, only their distal nephridioporal ends can be so compared. The more specialized kinds of nephridia have probably originated from the protonephridia, not as further specializations of them but rather by addition of extraneous elements; on the whole they are not homologous.

These more specialized nephridia with mesentoblastic constituents fall into two main groups.

The first of them consists of types 8 and 9, both of which have in common the union of an ectoblastic duct with the peritoneum but have no retroperitoneal mesentoblast. They are either urogenital, or are homodynamous with genital ducts (?also in the Enteropneusta). Their main difference is that in type 8 the peritoneal invagination is more pronounced as a rule, and that in type 9 the connectant cœlom has become exclusively excretory. These differences are not important, and these two types are in general homologous. Until retroperitoneal elements are discovered for them they must be considered distinct from the following; and to them the name *cœlonephridium* might be given.

The second kind of the more specialized nephridia comprises types 10 and 11, both characterized by the union of ectoblast with retroperitoneal mesentoblast. Type 11 differs from 10 by the addition of a cœlomostome (peritoneal funnel), in the manner made known particularly by the studies of E. Meyer and Goodrich. Their essential peculiarity is the retroperitoneal mesentoblast, not the peritoneal funnel. Hatschek (1888) classed these together with the preceding as metanephridia, and diagnosed them by the presence of a cœlomostome; but the difference with regard to the retroperitoneal element seems to me so important that these should be held distinct from the preceding, and in that case it would be well to limit the term metanephridium to types 10 and 11.

The three main kinds of nephridia that these considerations lead us to distinguish may be briefly compared as follows: *Protonephridium* (types 3, 4, 7), wholly ectoblastic or mesectoblastic (possibly in some cases both ectoblastic and mesectoblastic); *cœlonephridium* (types 8, 9), distal ectoblastic portion joining directly with a cœlomostome; *metanephridium* (types 10, 11), distal ectoblastic portion joining with retroperitoneal mesentoblast, and the latter connecting or not connecting with a cœlomostome. Only the second and third of these ever serve as genital ducts or are homodynamous with them. The metanephridium is the most complex because it may consist of as many as three elements, and it contains the smallest amount of the ectoblastic constituent.

The protonephridium in the course of transmutation and division of labor has not become entirely replaced, but it has rather become reduced in amount by the substitution of other elements for certain of its parts. And there have been two paths in this process. By the one, a relatively larger portion of the protonephridium has persisted and a cœlomostome has become directly connected with it, exemplified by the cœlonephridium. By the other a relatively smaller portion of it has maintained itself, to this has been added a secretory tube of retroperitoneal mesentoblastic tissue, and to the latter in some cases a cœlomostome, as illustrated by the metanephridium. The cœlomostome is homologically a genital funnel, as demonstrated by Meyer and Goodrich, comparable with a genital duct of, *e. g.*, a Nemertean. But what the retroperitoneal mesentoblastic element was originally, before it attached itself to a protonephridium, we are unable to decide; it may have originated from the outer layer, that outside of the peritoneum, of a primitive gonadal pouch.

We have now to see how these conclusions relate themselves to the views of other students. It will not be necessary to attempt a full historical review of the various opinions because a good discussion of them has been recently furnished by Lang (1903). There are two main views: (1) That the nephridia of all the Metazoa are essentially homologous, and (2) that those of the higher Metazoa are dyshomologous with the protonephridia.

The first of these has been maintained particularly by Lang (1881, 1884, 1903). To him the starting point is the condition in the Turbellarian *Gunda,* where there are continuous longitudinal main trunks, and more or less regularly arranged excretory ducts. He holds that such a condition has maintained itself in the case of the plectonephridia of the Hirudinea and Oligochæta, but that it has become modified in other Annelids by the segmentation of the longitudinal trunks. This idea is in a sense a necessary corollary of his view of the close relationship of the Turbellaria and Hirudinea. Besides the similarity in the Turbellaria and the Hirudinea above mentioned, he adduces the following main anatomical resemblances. (1) Hatschek's contention that in *Polygordius* the adult nephridia develop as outgrowths from a continuous longitudinal canal; the error of this observation has since been pointed out by Fraipont, Meyer, and Woltereck. (2) The presence of net-like nephridia (plectonephridia) in the Annelids; I have entered into the question of the homologies of these in the descriptive section upon the Oligochæta, and here need only recall that Vejdovský's embryological studies have shown that the plectonephric condition is secondary, derived from the meganephric. (3) The similarity in histological structure of the two kinds of nephridia. (4) Occurrence of serial provisory larval nephridia in Polychætes, that closely resemble protonephridia; that these are homologous with larval protonephridia as well as with the definitive ones, accordingly, that the protonephridia are homologous with segmental organs. Thus Lang derived (1903) "all the segmental nephridia of the Annelids from the segmental portions of the water vascular system that open externally, on the premise that in the Annelids those canals have not persisted which joined the successive segments of the water vascular system. Such a nephridial segment would have consisted in the ancestors of the Annelids of a pair of water vascular trees with excretory ciliated cells on the terminal ends of the capillary branches, and of a trunk opening outward.

. . . Since in the development of the Annelids the head end of the body precedes and the trunk with its successive segments first later comes to formation, so develops first the first nephridial tree pair, the head kidney adapted to the larval body, whose homology with the water vascular system is not contended even by the opponents of the unit theory, later perhaps a second and possibly still a third similar pair with reduced branching. This most anterior pair of nephridial trees that functions during the earliest larval life, at a time when there is still no secondary body cavity developed in the regions concerned, became in the phylogeny a transitory provisory structure, as can be demonstrated on so many larval organs, while the succeeding nephridial pairs of the trunk segments changed to segmental organs."

The other main view is that represented by Bergh (1885). According to him the larval nephridia of the Cœlomata are homologous with the protonephridia, while the adult nephridia of the Annelids are homologous with the gonadal ducts of the Platodes but not homologous with the protonephridia. Thus he concluded (as Williams did long before) that the segmental organs of Annelids were originally genital ducts and later changed into excretory organs; while the protonephridia do not communicate with the cœlom and never serve as genital ducts.

Goodrich has recently represented a view that in the main supports Lang's. To him there are "nephridia" proper that never serve as genital ducts; he considers all of these ectoblastic invaginations and essentially homologous. Then, adding materially to the discoveries of Eisig and E. Meyer, amplifying them, he find that upon such a nephridium a cœlomostome (peritoneal funnel, genital funnel) may become grafted, giving rise then to a complex "nephromixium." To Goodrich all nephridia are essentially homologous, they differ only in being combined or not combined with a cœlomostome.[15] His argument like Lang's is rather anatomical than embryological. Both of these investigators also lay great stress upon the presence in Annelid nephridia of the solenocytes, cells similar to the flame cells of protonephridia; Goodrich argues that such com-

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[15] In the descriptive part under the caption of Polychæta, Goodrich's ideas are given more *in extenso*.

plex cells could not have arisen independently in the two groups, rather that their presence in them means homology of the organs concerned.

It will be seen that my views do not coincide exactly with any of the preceding. I agree entirely with Meyer and Goodrich that the cœlomostome is an organ of origin independent from the nephridium, one that in some cases may connect with the latter. This cœlomostome is equivalent to the genital duct of a lower metazoan, as shown by Bergh. I agree also with Lang that the excretory ducts of the protonephridia have maintained themselves in part in the higher Metazoa, and that the longitudinal canals have disappeared. But I have tried to show that while sometimes such an excretory duct joins directly with a cœlomostome, forming what I call a cœlonephridium, in other cases it joins with retroperitoneal mesentoblastic tissue and the latter may secondarily join with a cœlomostome (metanephridium). In other words, we have to reckon with a retroperitoneal element that frequently forms the greater portion of the nephridium, and this is what Lang and Goodrich have failed to take into account. And I differ from Bergh in concluding that the metanephridium is not in its entirety equivalent to a genital duct, but that only a portion of it (the cœlomostome) is. Goodrich's mistake, if my interpretation is correct, is in assuming that there are only two elements, ectoblastic tube and peritoneal cœlomostome; he entirely neglects the retroperitoneal tissue, and yet this is just what shows the dyshomology of protonephridium and metanephridium. It is a mistake that has resulted from too exclusive reliance upon phenomena of adult structure with neglect of comparative embryology. And the arguments from histological similarity, intracellular cavity, similarity of solenocytes to flame cells, etc., can have little weight now that we are acquainted with still more striking cases of histological convergence as notably the case of the Malpighian vessels of Insects and those of Arachnids. Goodrich has excellently analyzed the history of the cœlomostome and has thereby greatly clarified our knowledge of nephridia. But he has omitted entirely from his general conclusions the retroperitoneal element which has come to supplant the protonephridium almost entirely thus excluding the homology of the protonephridium and metanephridium.

It will be noted that in my considerations I have entirely excluded the argument from the side of the recapitulation theory, for I have maintained (1906) that this theory is fundamentally erroneous. I have compared corresponding stages, adult or embryonic, of the different groups, have stressed embryological resemblances, but have not compared an adult stage of one organ with an embryonic one of another.

It might be expected that I should now enter upon the question of the phylogenetic significance of the cœlom, because this space has so often a close anatomical connection with nephridia. But I have nothing new to add to the discussion, and for a good representation of it would refer to the treatments by E. Meyer (1901) and Lang (1903). I need only state that there are three main theories in explanation of the origin of the cœlom. The oldest was founded by Sedgwick, and is to the effect that the cœlom is an enterocœlic diverticulum, referable to a gastral pocket of an anthozoan. This has deservedly received little support. Next came the gonocœl theory, foreshadowed by Hatschek, elaborated particularly by Bergh and E. Meyer, and more recently supported by Lang and Goodrich; it concludes that the cœlomic sac of a higher metazoan is the amplified derivative of the genital pouch (gonad) of such a form as a Platode, therefore that the mesentoblast is referable to germ cells The third view is the nephrocœl theory, founded by Faussek (1901) and Ziegler (1898), that the cœlom was originally an excretory organ and that the germ cells have associated themselves secondarily with it. Of these three theories the gonocœl theory seems to me to receive the fullest support from the facts of anatomy and embryology.

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